VARIABLE PROCESSING OF FLAVOURS IN RAT STM

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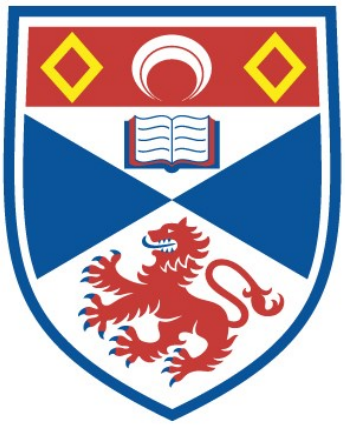

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Variable processing of flavours in rat STM

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The composition of this thesis and the research reported therein are the unaided work of the author and have not previously been submitted for the award of a higher degree.

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A series of experiments examined the consequences for habituation and conditioning phenomena of presenting rats with two novel flavour solutions, A and B. Various solutions, differing in their degree of similarity to one another, were used as A and B. The initial duration of exposure to each solution was 5-min and presentation of B immediately followed withdrawal of A. Controls either received (i) only A, (ii) only B, or (iii) both A and B, but unpaired. A 10-min test administered 6 hours after the A-B paired presentation found that (in comparison to that shown by controls) the attenuation of neophobia (AN) to solution A was enhanced (Expts. 1, 6a and 7a) and AN to solution B reduced (Expts. 8 and 9) when A and B were similar, but when A and B were dissimilar, AN to A was reduced (Expts. 3, 4 and 6b) and AN to B unaffected (Expts. 8 and 9). When A was paired with LiCl 4 hours after the A-B paired presentation and rats were subsequently tested for their aversion to A, B was found to have no influence on the amount of latent inhibition exhibited towards A. This was so, regardless of whether B was similar (Expt. 10b) or dissimilar (Expt. 10a) to A. Moreover, B did not disrupt latent inhibition to A even when AN to A was reduced by B, as indicated by a comparison of the amount of A consumed on the conditioning trial by experimental and control rats (Expt. 11c). Finally, when the single A-B paired presentation was followed by injection of LiCl and rats were subsequently tested with solution A, the conditioned aversion to A was potentiated by B when A and B were similar (Expt. 12b), but overshadowed by B when A and B were dissimilar (Expt. 12a). It is suggested that the data reported here can best be accommodated by Wagner's (1976) model of stimulus processing.

Summary

The research reported in this thesis examines factors that affect the willingness of rats to ingest novel flavour solutions. Emphasis is placed on the memorial processes assumed to underlie the decision as to whether or not a solution is "safe" (c.f., Kalat & Rozin, 1971; 1973) to drink.

Rats exhibit caution (neophobia) in consuming an unfamiliar (target) solution. This unconditional response to novelty habituates as the rat acquires experience with the target solution (provided that ingestion of the target solution has no noxious consequences!). Neophobia to the target solution may be restored, however, if another (distractor) solution is presented during the interval separating preexposure to, and testing of, the target solution (Green & Parker, 1975). In Section 1, the phenomena of habituation to an iterated target stimulus and the disruption of this process by a distractor are introduced. Theoretical explanations of the "dishabituation" effect of a distractor stimulus (e.g., Groves & Thompson, 1970; Pavlov, 1927; Robertson, 1980; Wagner, 1976) are described and assessed. The possibility of an empirical test of the relative validity of the Robertson and the Wagner hypotheses using the attenuation of flavour neophobia procedure of Green and Parker provided the

impetus for the experiments reported in Section 2.

In Section 2, hooded Lister rats were shown to exhibit less neophobia towards (i.e., drink more of) a novel fluid (3% lemon or 5% sucrose) on a 10-min test if given a 5-min exposure to that fluid 6 h earlier. Presentation of a distractor (1.25% coffee) immediately after preexposure to the test solution enhanced neophobia habituation to lemon (Expt. 1), but disrupted habituation to sucrose (Expt. 3). This bidirectional distractor effect was not due to distractor-induced change in the hedonic value of the preexposed test flavour (Expt. 4). Evidence was obtained (Expt. 5) indicating that the rat perceives lemon to be more similar to coffee than is sucrose. It is suggested that when test flavour and distractor are dissimilar, processing of the distractor denies the preexposed test flavour sufficient processing in STM to allow encoding of information about that flavour in LTM. Consequently, the rat responds to a subsequent presentation of the test flavour as it would to a novel stimulus. When test flavour and distractor are similar, however, the distractor elicits less processing in STM (c.f., Wagner, 1976) and is therefore less able to disrupt STM processing of the preexposed test flavour. The resultant loss of neophobia to the test flavour resulting from encoding of information about that flavour in LTM may then be augmented by generalization of attenuated neophobia to the distractor. Consistent with this analysis, coffee was shown to suffer more proactive

interference when preceded by lemon than when preceded by sucrose (Expt. 8).

The bidirectional distractor effect observed in Expts. 1 and 3, and the differential vulnerability of the distractor to proactive interference from similar or dissimilar solutions that was observed in Expt. 8 were replicated in Expts. 6a and 6b, Expt. 7a, and Expt. 9 using solutions (i.e., 3% cider vinegar, 50% evaporated milk, 3% grape juice, and 1.5% HCl) whose degree of similarity to each other was known a fortiori (c.f., Parker & Revusky, 1982).

In Section 3, attention is drawn to the similarity of the procedure designed to establish habituation and that intended to establish latent inhibition to a stimulus. A limited review of empirical data is presented testifying to the fact that habituation and latent inhibition are affected similarly by identical parameter manipulations. The Wagner (1976) model views habituation and latent inhibition as the outcome of a common underlying process. Expts. 10a and 10b, therefore, sought to determine whether latent inhibition of a conditioned taste aversion (CTA) to lemon or sucrose solution would be affected by a coffee distractor in a manner consonant with predictions derived from the results of the neophobia experiments reported in Section 2. The distractor, however, had no effect on strength of latent inhibition in either experiment. Expt. 11c demonstrated

that it is possible for a distractor (30% vanilla) to disrupt attenuation of neophobia to a target flavour (3% cider vinegar) without affecting latent inhibition to the target flavour, i.e., there is no direct correspondence between measures of habituation and latent inhibition to the same stimulus.

In Section 4, the phenomena of overshadowing and potentiation of a CTA are introduced. At least one explanation of potentiation (c.f., Durlach & Rescorla, 1980) stresses the importance of an association between the elements of a compound CS. Rescorla and Furrow (1977) found interstimulus associations were formed more rapidly between similar rather than dissimilar stimuli. Given these results, Expts. 12a and 12b sought to determine whether a single sequential presentation of lemon and coffee (similar solutions) paired with LiCl would result in potentiation of a conditioned aversion to the lemon solution and whether a single sequential presentation of sucrose and coffee (dissimilar solutions) paired with LiCl would result in overshadowing of a conditioned aversion to the sucrose solution. These experimental predictions were confirmed.

In Section 5, a potential confound in the neophobia experiments is addressed. Interpretation of attenuated neophobia as an habituation process is defended and alternatives to the Wagner (1976) theory of habituation are considered for their ability to encompass the data reported

in Section 2. Only the Wagner model, however, appears able to account for all the data. Nevertheless, some limitations of the model are indicated. Finally, the conditions promoting overshadowing and potentiation of a CTA are discussed. The value of further research is indicated.

CONTENTS

1 INTRODUCTION

1.1 Habituation and dishabituation

The unconditional response (UR) elicited by an initially novel stimulus diminishes with repeated presentation of that stimulus. This phenomenon, called habituation, has been observed in almost every species studied (Harris, 1943; for more recent reviews of habituation see Groves & Thompson, 1970; Horn & Hinde, 1973; Peeke & Herz, 1973; Thompson & Spencer, 1966; Tighe & Leaton, 1976).

Thompson and Spencer (1966) identified nine parametric features characteristic of habituation. The research reported here was primarily concerned with the eighth item on their list, viz., "presentation of another (usually strong) stimulus results in recovery of the habituated response (dishabituation)."

1.2 Dishabituation: an example of sensitization?

Pavlov (1927) believed that the decline in the strength of the UR to an iterated target stimulus was the necessary consequence of a concomitant growth in the central nervous system of a process that specifically inhibited responding to the target stimulus. A distractor (dishabituatory)

stimulus restored responding to an habituated target stimulus by inhibiting this inhibitory process, i.e., "disinhibition".

If, as Pavlov believed, a distractor acts uniquely on a specific target stimulus to remove habituation to that stimulus, then a number of predictions follow (see Thompson & Spencer, 1966; pg 27). Firstly, dishabituation should not increase the habituated response above its control level, i.e., the magnitude of the UR to the target stimulus prior to habituation training. Secondly, in the absence of further habituation trials, a dishabituated response should remain at a high dishabituated or control level. Thirdly, a distractor should not increase responding to stimuli that have not undergone habituation. None of these predictions, however, have received empirical support.

Habituation of the unconditional startle response of the rat to an auditory stimulus, e.g., a tone, is dishabituated by interpolation of a flashing light between iterated presentations of the tone. On the first trial after presentation of the distractor, the magnitude of the UR to the tone is greater than that observed to the tone prior to habituation. This elevated response to the tone spontaneously returns to the habituated level (Groves & Thompson, 1970). In addition, the unhabituated hindlimb flexion reflex of the acute spinal cat in response to a brief train of electric shock to the skin is elevated well

above control levels by delivery of a strong shock train elsewhere on the limb (Thompson & Spencer, 1966).

These results suggest that dishabituation is not the removal of an inhibitory process responsible for habituation to a specific stimulus, but rather the superimposition of an independent process which produces a non-specific increase in responding to all stimuli, viz., sensitization. Such evidence led Groves and Thompson (1970) to propose their influential "dual-process" theory of habituation; according to which, the magnitude of responding to a stimulus is a function of two processes. Firstly, the level of activity in the S-R pathway "which is the most direct route through the central nervous system from stimulus to response" and secondly, the general level of excitation or arousal (i.e., "state") of the organism. Habituation is thought to occur in the S-R pathway while sensitization affects the "state". Although independent processes, habituation and sensitization interact to produce the final behavioural outcome.

1.3 "True" dishabituation: an example

Recently, Whitlow (1975) reported data that support the possible operation of dishabituation separate from sensitization (i.e., "true" dishabituation). In the Whitlow (1975) study, the unconditional vasoconstriction response of the rabbit to a novel tone was attenuated when preceded by

prior presentation of that same tone, but not when preceded by presentation of a different tone. More importantly, interpolation of a visual-tactile (distractor) stimulus between presentation of the target tone and the preceding comparison tone produced an increase in the UR to the target tone when the comparison and target tones were identical, but not when they were different, i.e., the distractor removed a stimulus-specific response decrement without appearing to have a general sensitizing effect.

1.4 Wagner's (1976) model

The Whitlow data cannot be readily handled by the dual-process theory which postulates a non-specific energizing effect of a distractor. However, Wagner's (1976) model of stimulus processing, formulated to account for habituation and conditioning phenomena, provides a mechanism by which to explain these results. The Wagner model assumes that incoming information enters into a transient limited-capacity short-term memory (STM) where it undergoes processing prior to its transfer to a less transient, relatively unlimited-capacity long-term memory (LTM). The more processing a stimulus receives in STM the greater is the likelihood of its transfer to LTM; in the absence of any such processing, a stimulus undergoes a rapid decay from STM.

The extent to which a stimulus is already represented (i.e., primed) in STM prior to its occurrence is assumed to determine the extent to which presentation of that stimulus will lead to processing of the stimulus input. If STM is primed with (i.e., contains information about) a stimulus, either via a prior presentation of that same stimulus (self-generated priming) or via retrieval of a memorial representation of that stimulus from LTM through the action of cues associated with it (retrieval-generated priming), then the actual occurrence of the stimulus will be less likely to engage the rehearsal mechanism and less likely to elicit a behavioural response. Thus, habituation of the UR to a target stimulus occurs because STM is primed with information about that stimulus prior to its actual occurrence; consequently, presentation of the target stimulus is not surprising and does not elicit an UR.

According to the Wagner model, the limited capacity for processing temporally contiguous stimuli that characterizes STM means that the processing demanded by a distractor necessarily curtails the amount of processing a preceding stimulus is able to receive in STM. This reduces the likelihood of any self- or retrieval-generated priming of STM prior to the next presentation of the target stimulus. Consequently, the discrepancy between the representation of the target stimulus entering into STM and the representation of that stimulus already present in STM will be greater for

subjects that experience a distractor than will be the case for subjects that do not. Since the amount of processing a stimulus receives is inversely related to the amount of information about that stimulus already present in STM, subjects that experience a distractor are therefore more likely to exhibit an UR to the target stimulus than are subjects preexposed to the target stimulus without a distractor.

The Wagner model would thus account for the Whitlow (1975) data by assuming that presentation of the visual-tactile stimulus removed information about the preceding tone from STM thereby preventing a priming-induced decrement in responding to the target tone.

Evidence of apparent dishabituation (as opposed to sensitization) has also been reported by Green and Parker (1975). Green and Parker found that the reluctance of rats to consume a novel flavour (i.e., neophobia) was attenuated by a brief exposure to that flavour six hours prior to the test of neophobia. (This long interval between preexposure and testing makes it likely that AN to the target solution during testing was due to retrieval-generated rather than self-generated priming of STM). Rats that experienced a second novel flavour immediately after preexposure to the target flavour, however, showed an increased reluctance to ingest the target flavour on a subsequent occasion compared to rats preexposed to the target flavour without a

distractor.

Unfortunately, Green and Parker did not include a group preexposed to the distractor only and subsequently tested for neophobia to the target flavour. Such a control would have commented directly on the possibility that the distractor effect obtained in their study reflected a sensitization process. Other studies, however, have found no evidence that prior presentation of one flavour produces greater neophobia to a different target flavour (i.e., sensitization) than that shown by rats presented only with the target flavour. Instead, the opposite appears to be the case; preexposure to a novel flavour different from the target flavour reduces neophobia towards the latter (Braveman & Jervis, 1978; Siegel, 1974).

Further reason to doubt that the Green and Parker distractor effect was due to sensitization rather than dishabituation derives from the fact that the distractor employed by Green and Parker was maximally effective in disrupting habituation to the target flavour the closer the temporal proximity of the distractor to the target flavour during the preexposure phase. Such a temporal gradient of distractor effectiveness, while consistent with the assumptions of the Wagner (1976) model, is contrary to what one would expect if the distractor effect was due to sensitization. If the latter were the case, maximal dishabituation ought to have occurred not when the

distractor immediately followed presentation of the target flavour during the preexposure phase, but when the distractor immediately preceded the test presentation of the target flavour. For these reasons, the Green and Parker (1975) results appear more reasonably attributed to dishabituation than to sensitization.

1.5 Robertson's (1980) hypothesis

Recently, Robertson (1980) proposed an alternative to the Wagner interference hypothesis of a distractor's mode of action. Robertson suggested that the processing capacity of animal STM may not be so limited as to prevent conjoint processing of a target stimulus and a temporally contiguous distractor. If that is the case, when a short interval separates the preexposure and test presentations of the target stimulus, such that the stimulus or stimuli presented during the preexposure phase are likely still to be represented in STM when the test trial is administered, one would expect animals that experienced a distractor to exhibit a greater UR to the target stimulus during testing than do animals preexposed to the target stimulus only. This would be because a comparison of the target stimulus during testing with the contents of STM would occasion greater generalization decrement for the former group, for whom STM is primed with information about both the preexposure presentation of the target stimulus and the distractor, than would be the case for the latter, for whom

STM is primed with information about the preexposure presentation of the target stimulus only. Hence, the test presentation of the target stimulus would likely be regarded as a less familiar stimulus by animals that received a distractor during the preexposure phase than by those preexposed to the target stimulus only.

The target stimulus and distractor might be processed simultaneously, but independently of one another during the preexposure phase; each forming a separate association with accompanying contextual cues. Alternatively, the target stimulus and the distractor might themselves become associated and the resultant configural stimulus become associated with the contextual cues. In either event, when a comparatively long interval separates the preexposure and test presentations of the target stimulus, i.e., when self-geneerated priming of STM is unlikely to be operating, one would predict animals preexposed to the target stimulus with a distractor to exhibit a greater UR to the target stimulus during subsequent testing than do animals preexposed to the target stimulus only. This would be because contextual cues retrieve either independent representations of the preexposed target stimulus and the distractor, or a configural stimulus of which the preexposed target stimulus and the distractor are component parts, from LTM into STM. A comparison of the test presentation of the target stimulus with the contents of STM would thus occasion greater generalization decrement for animals that

experienced a distractor during the preexposure phase than it would for animals preexposed to the target stimulus only. Hence, the test presentation of the target stimulus would be less familiar to the former than to the latter group.

Although it makes no difference to the outcome predicted during testing whether the target stimulus and the distractor (while not forming an association with each other) each form an association with accompanying contextual cues during the preexposure phase or whether the target stimulus and the distractor form an association with each other and the resultant configural stimulus is then associated with the contextual cues, there are grounds for believing the latter to be the more accurate description of events. If all that is important in order to obtain a retrieval-generated priming decrement in the magnitude of the UR exhibited to a preexposed target stimulus is that the target stimulus and the distractor each have formed an association with contextual cues so that reexposure to those contextual cues on the test trial retrieves information about both the target stimulus and the distractor from LTM into STM, then there need be no necessary relationship between the target stimulus and the distractor during the preexposure phase, i.e., the effectiveness of the distractor in disrupting habituation to a target stimulus should not depend on the relative temporal contiguity of the distractor to the target stimulus during the preexposure phase.

However, the distractor does seem to depend on close temporal proximity to the preexposed target stimulus in order to maximally disrupt habituation to the latter (Green & Parker, 1975). This argues against the hypothesis that target stimulus and distractor are processed independently in STM during the preexposure phase, each forming a separate association with contextual cues, but is consistent with the hypothesis that target stimulus and distractor are processed as a configural stimulus which is then associated with contextual cues during preexposure.

The Green and Parker (1975) and the Whitlow (1975) data can be readily explained by both the interference and the association hypothesis. Although there is no experimental evidence at present to separate the two hypotheses, there is reason to believe, however, that the association hypothesis may provide the more accurate description of the process underlying the distractor effect.

Suggestive evidence for the validity of the association hypothesis of a distractor's mode of action comes from studies of sensory preconditioning. In sensory preconditioning, two stimuli are presented sequentially and evidence that an association has been formed between them is demonstrated by subsequently pairing the second stimulus with a US and then testing the first stimulus for its ability to elicit a CR (Brogden, 1939). That an association is formed between temporally proximate stimuli (Brogden,

1939; Thompson, 1972) encourages the belief that an association is likewise formed between a temporally proximate target stimulus and distractor.

2 ATTENUATION OF NEOPHOBIA (AN)

When confronted with a novel food, rats typically avoid or sample only a small portion of it (Barnett, 1963; Chitty, 1954). This response is known as neophobia.

2.1 Individual and strain differences

Wild rats exhibit a much stronger avoidance of novel substances than do laboratory rats; among the latter, hooded-rats exhibit greater neophobia than do albino rats (Mitchell, 1976). In addition to between-strain variation in strength of neophobia, individual rats of the same strain also differ in the degree of neophobia they exhibit towards novel edibles (Archer & Sjoden, 1979; Mitchell, 1976; Robertson, 1982). Recent evidence suggests that the latter are related to the social dominance of the rat. When pairs of fluid-deprived rats were allowed to compete for access to a single drinking bottle that delivered familiar tap water, one member of each dyad was able to consistently obtain more fluid than its rival during a two-minute trial. However, when the drinking bottle delivered not familiar tap water, but novel 3% vinegar solution, the positions were reversed, i.e., rats that were dominant over their rival when competing for water drank less fluid than the other member of the dyad when both competed for access to novel vinegar solution (Robertson, 1982).

2.2 Experiential factors

Although the disposition to avoid novel stimuli is genetically determined (Barnett, 1963; Mitchell, 1976), the strength of neophobia exhibited by a rat may be influenced by experiential factors. For example, handling in infancy results in adults that are less neophobic than are non-handled control rats (Weinberg, Smotherman & Levine, 1978). In contrast, a rat that suffers toxicosis after sampling a novel food and survives will exhibit a relatively short-lasting heightened neophobia towards novel foods in general (Best & Batson, 1977; Domjan, 1975), and a more durable avoidance of the particular novel food sampled prior to experiencing toxicosis (Garcia & Ervin, 1968). This latter response will generalize to other novel foods that are similar to the food that produced the internal malaise (Domjan, 1975; Parker & Revusky, 1982).

2.3 Adaptive function

Since rats are omnivorous and many edible substances may contain either naturally occurring toxins or toxins implanted by Man as an attempted pest control measure, it is likely that the rat may on occasion eat a potentially lethal substance. Many animals, including Man, can minimize, to a certain extent, the harmful consequences of ingesting toxic material by ejecting the offensive substance from the body

by vomiting. The rat, however, can not do so: a sphincter muscle makes it physiologically impossible for the rat to vomit (Garcia & Ervin, 1968). The adaptive value, to the rat, of exhibiting caution towards novel, potentially hazardous food substances is therefore readily apparent: if the substance contains toxin, the rat, if it is fortunate, will not have consumed enough to endanger life.

2.4 Memory demands

A novel food will be avoided on a subsequent occasion if a first sampling resulted in toxicosis. However, if a novel food has no unpleasant aftereffects, then more of that particular food will be consumed on a subsequent occasion, i.e., neophobia towards that food habituates. To respond appropriately to a novel food on the basis of previous experience of the aftermath of consuming that substance, the rat must be able to recognize that food as familiar on the second occasion it is encountered. In other words, information about the particular sensory characteristics of a novel food, together with information about the consequences of consuming that food, must be represented, in some fashion, in rat memory and this stored information used to determine whether subsequently encountered foods have been previously experienced and whether they should therefore be treated with caution or readily consumed. Green and Parker (1975) demonstrated that the process responsible for encoding information about a novel target

solution and the consequences of ingesting it in rat memory was susceptible to interference if the rat consumed a different (distractor) novel fluid immediately after sampling the target solution.

Habituation of neophobia towards novel solutions that were followed by no noxious consequences was therefore chosen as the paradigm within which to investigate the relative merit of the Wagner (1976) and the Robertson (1980) hypotheses regarding the mode of action of a distractor (a) because the procedure promised to be relatively simple, (b) the experimental task and the response demanded of the rat are both ones that are ecologically important to the rat (c.f., Seligman, 1970), and (c) prior evidence existed as to the possibility of a distractor effect being obtained with this procedure (Green & Parker, 1975).

2.5 PRESENT STUDIES

2.5.1 Experiment 1

While there is reason to favour the association rather than the interference hypothesis of the dishabituation effect of a distractor, experimental data to support such a preference would be desirable. The procedural similarity between sensory preconditioning studies and studies of habituation that employ a distractor has been noted. If the association hypothesis is correct one might therefore expect

a change in the response elicited by the target stimulus from one test to another as a result of an intervening operation on the distractor. The interference hypothesis would not make this prediction. As a prelude to employing such a procedure to investigate the relative merit of the rival explanations of the dishabituating effect of a distractor stimulus, it was decided to replicate the Green and Parker (1975) study using different novel fluids from those used in that study in order to test the generality of the effect reported by Green and Parker. The solutions used in Expt. 1 (i.e., 3% lemon and 1.25% coffee), and the relative concentration of each, were chosen because they have been commonly used in studies of neophobia and taste aversion learning, and were readily available commercially. Lemon was chosen as the target solution in Expt. 1 because pilot work (see Table 1) had demonstrated that rats given a 5-min presentation of 3% lemon (i.e., Group P) would drink reliably more lemon on a 10-min test six hours later than would rats with no experience of drinking lemon solution prior to the 10-min neophobia test (i.e., Group NP). The coffee solution was chosen as the distractor because pilot work (see Table 1) had indicated that this too was a salient solution to the rat. Green and Parker (1975) interpreted their finding that AN reached asymptote 4-6 hours following preexposure to a target solution as an indication that consolidation in LTM of information about the preexposed target solution was complete at this time. A 6 hour interval separating preexposure and test presentations of

the target solution was chosen in Expt. 1, and in subsequent neophobia experiments, therefore, in the belief that any AN observed would thus be the consequence of retrieval- rather than self-generated priming of STM.

Table 1

Results of pilot studies

	Mean Intake				
	Group				
Solution	NP	P	t	df	p
0.75% coffee	6.2	6.9	1.01	14	ns
1.25% coffee	4.4	6.3	2.98	13	**
3.0% lemon	4.3	7.0	4.05	14	****
5.0% sucrose	8.3	10.2	2.29	12	*

Note. * = <.05, ** = <.01, *** = <.001, **** = < .0001
ns = not significant

In addition to the solutions used, Expt. 1 differed from the Green and Parker study in other procedural details, including; subjects (Lister vs Wistar rats); context in which novel fluids were presented (drinking chamber vs home cage); and type of test (single-bottle vs two-bottle presentation).

Method

Subjects

Twenty-four experimentally-naive male Lister rats (165-232 g) bred in the Psychology Dept., University of St. Andrews were housed in wire-topped plastic cages with dry

food pellets continuously available. The room in which the rats were maintained was illuminated on a 12:12-h light/dark cycle (lights on at 0700 h).

Apparatus

Testing took place in four open-topped boxes (25 x 25 x 40 cm) made of black Perspex with a grid floor. A 50 ml calibrated drinking tube was attached to the outside front wall of the test box by a steel clip, with the nozzle protruding into the box via a hole situated 10 cm from the side and 6 cm from the floor of the box. The test boxes were situated in a room separate from that in which the home cages were housed.

Procedure

Three days prior to the start of Expt. 1, access to water in the home cage was restricted to the period 1530-1600 h. On experimental Days 1-3 (commencing at 1530 h), each rat was placed in the test box for 10-min and allowed to drink from the calibrated drinking tube. This was intended to habituate rats to the apparatus. Following removal from the test boxes, the rats were returned to the home cage and given 20-min access to water. The amounts of water drunk in the test box on Days 1-3 were averaged for each rat and divided by its weight. The resulting ratios were rank-ordered and used to assign rats to three groups of eight rats each (i.e., Group PD = Preexposed with Distractor; Group P = Preexposed; Group NP = Not Preexposed).

Each rat in Group P and in Group NP was matched as closely as possible in terms of weight with a rat in Group PD. Commencing at 0930 h on Day 4, the test day, Group PD was given a 5-min presentation of novel 3% (v/v) lemon solution followed immediately by a 5-min presentation of novel 1.25% (w/v) coffee solution. Group P received a similar 5-min presentation of lemon solution followed immediately by presentation of tap water. Each rat in Group P was removed from the test box as soon as it had consumed an amount of water equivalent to the amount of coffee drunk by its matched-weight control in Group PD. The third group, Group NP, drank only water during preexposure; each rat in Group NP being removed from the test box as soon as it had consumed an amount of water equivalent to the total amount of lemon and coffee solution consumed during preexposure by its matched-weight control in Group PD. Six hours later, the rats were returned to the test box and presented with the 3% lemon solution. The amount consumed during a 10-min period was recorded.

Results and Discussion

The three groups did not drink equivalent amounts of lemon on the 10-min test (see Figure 1). A oneway ANOVA confirmed that these differences were reliable ($F(2, 21) = 9.88$, $p < .001$). Pair-wise comparisons using Duncan's Multiple Range Test (DMRT) indicated that Group NP drank

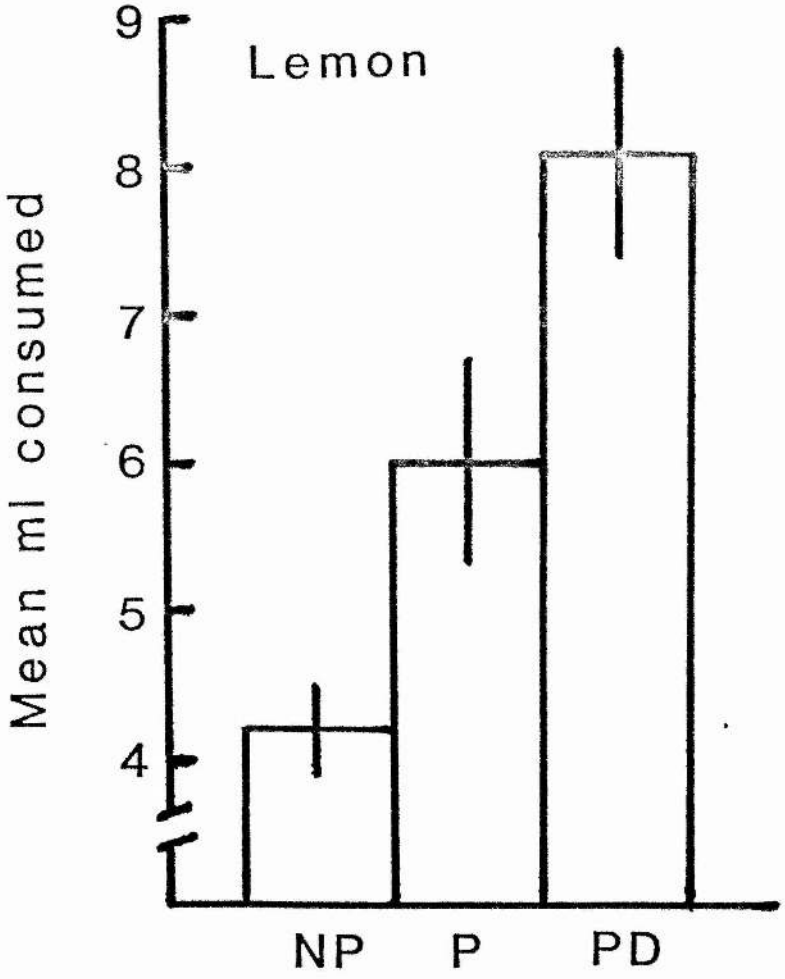

FIGURE 1. Mean consumption (ml) of target solution by groups P, PD and NP on the 10-min neophobia test in Experiment 1. The vertical lines bisecting the bars in Fig. 1, and in subsequent Figures, represent SEMs.

significantly less lemon (4.19 ml) than the amount (6.11 ml) consumed by Group P ($p < .05$) and significantly less than the amount (8.06 ml) drunk by Group PD ($p < .01$). Thus, preexposure to the test flavour attenuated neophobia to that flavour on a subsequent occasion (Group P versus Group NP) as was reported by Green and Parker (1975). The most interesting outcome of Experiment 1, however, was the performance of Group PD, which drank significantly more lemon than did Group P ($p < .05$).

The enhanced attenuation of neophobia exhibited by Group PD in Experiment 1 is contrary to the result of the Green and Parker (1975) study which found that a distractor disrupted attenuation of neophobia to a preexposed novel flavour, and is inconsistent with both the associative and the interference hypothesis of a distractor's mode of action. Both these hypotheses predicted dishabituation to occur; the associative hypothesis because the test presentation of the lemon solution involved greater generalization decrement for Group PD than for Group P and hence should have been more novel and elicited more neophobia for Group PD than for Group P; the interference hypothesis because the distractor disrupted STM processing of the lemon solution during the preexposure phase, thereby preventing any self- or retrieval-generated priming of STM prior to the test presentation of the lemon solution in the case of Group PD. Since neither of these hypotheses accounts for the enhanced habituation of neophobia produced

by the distractor in Experiment 1, some other explanation of this result must be sought.

2.5.2 Experiment 2

A number of experimental manipulations have proven effective in attenuating flavour neophobia in rats. For example, handling in infancy (Weinberg *et al*, 1978); experience of novel environments (Braveman, 1978); prior presentation of flavours other than the target flavour (Braveman & Jervis, 1978; Capretta, Petersik, & Stewart, 1975; Siegel, 1974); and prior exposure to various odours (Hennessy, Smotherman, & Levine, 1977) all reduce neophobia to a target flavour. These experiments appear to suggest that prior experience of novel stimulation (regardless of its nature) is sufficient to attenuate flavour neophobia in rats. Accordingly, it was decided to test the hypothesis that Group PD showed less neophobia to the lemon solution than did Group P in Experiment 1 because Group PD drank more novel fluid during the preexposure phase than did Group P.

If the enhanced attenuation of neophobia observed in Experiment 1 was the result of Group PD drinking more novel fluid during preexposure than did Group P, then ensuring equivalent intake of novel solution during the preexposure phase should eliminate this effect. Accordingly, three groups of rats were given a 10-minute test of neophobia to the lemon solution. Two of these groups, i.e., Group PD

and Group P, were treated in much the same way as the corresponding groups of the same name in Experiment 1, with the exception that Group P did not receive a water distractor after preexposure to lemon, and the amount of lemon and coffee solution drunk by Group PD during preexposure was not allowed to exceed the amount of lemon solution drunk by Group P. The third group, Group G, was preexposed to an amount of coffee solution equivalent to the amount of lemon drunk by Group P during preexposure. Group G was added to test whether the attenuation of neophobia to lemon observed in Group P depended upon prior exposure to the lemon solution.

Method

In all unspecified details, the procedure and apparatus in Experiment 2 were identical to those of Experiment 1.

Subjects

Eighteen experimentally-naive female Lister rats (116-198 g), bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as rats in Experiment 1.

Procedure

Each rat in Group P was matched with a rat of similar weight in Group PD and Group G (where G = genaralization). A 23.5 hour per day water deprivation schedule was

introduced six days prior to testing. On the test day, rats in Group P (n = 6) were given a 5-min presentation of 3% (v/v) lemon solution. Rats in Group G (n = 6) were presented with 1.25% (w/v) coffee solution, and rats in Group PD (n = 6) were presented with the lemon followed immediately by an equal amount of coffee solution. The total amount of fluid that rats in Group G and Group PD drank during the preexposure phase was not allowed to exceed the amount of lemon solution drunk by matched-weight control rats in Group P. Six hours later, all rats in each group were given a 10-min presentation of lemon solution.

Results and Discussion

It is clear from Figure 2 that the 3 groups did not differ in the amount of lemon solution (means 3.20-3.85 ml) they drank on the neophobia test. This was confirmed by a oneway ANOVA ($F(2, 15) = .69$, $p > .10$). That Group PD did not differ from Group P supports the hypothesis that the enhanced habituation of neophobia towards the lemon solution exhibited by Group PD, relative to that shown by Group P, in Expt. 1 was the result of Group PD drinking more novel fluid during the preexposure phase than did Group P, i.e., experience of novelty per se reduces neophobia towards a novel fluid. The comparable amount of lemon ingested by Group P and Group G is consistent with this hypothesis, indicating, as it does, that the strength of neophobia exhibited towards lemon is little influenced by the identity

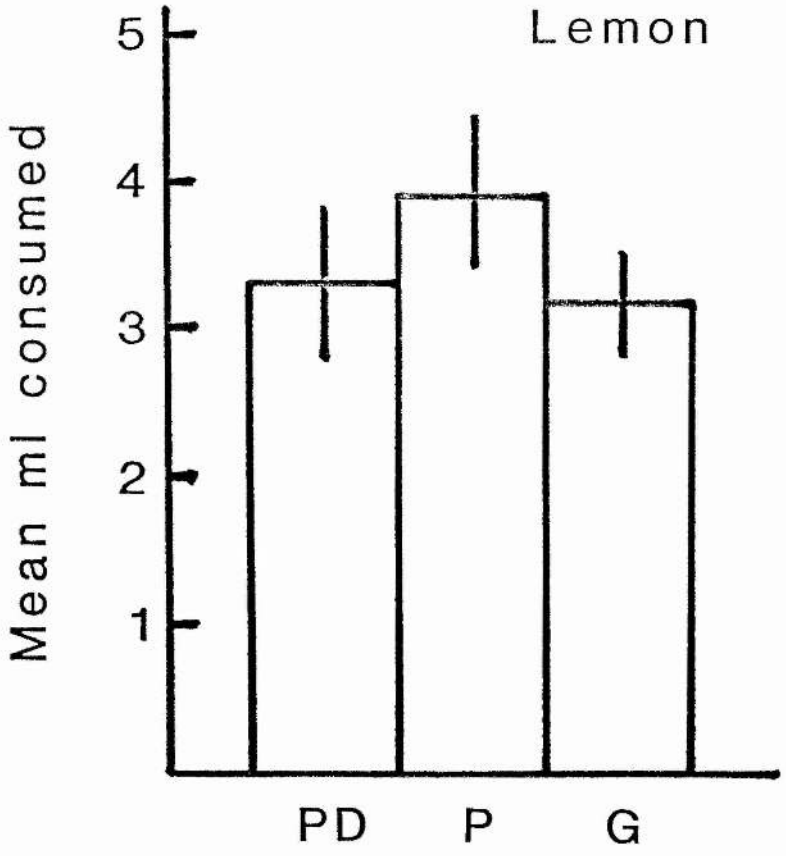

FIGURE 2. Mean consumption (ml) of target solution by groups P, PD and G on the 10-min neophobia test in Experiment 2.

of the solution experienced during the preexposure phase.

Such an explanation of the enhanced habituation effect obtained in Experiment 1 is, however, unsatisfactory in one important respect: it does not explain why rats given a distractor in the Green and Parker (1975) study did not show a similar enhanced attenuation of neophobia given that they also experienced more novel fluid during preexposure than did rats preexposed to the target solution without a distractor. With this in mind, an alternative interpretation of the performance of Group G in Experiment 2 is of particular interest. The comparable amount of lemon solution drunk by Group G and Group P may indicate that to the rat a 3% lemon solution is sufficiently like a 1.25% coffee solution that loss of neophobia to one solution generalizes to the other. Group PD may have shown less neophobia than did Group P in Experiment 1, therefore, because loss of neophobia to the distractor generalized to the target solution and summated with loss of neophobia to the preexposed target solution itself.

It is important to recognize, however, that the enhancement effect observed in Experiment 1 cannot be attributed solely to loss of neophobia to the distractor generalizing to the target solution on the neophobia test. If the distractor was effective in preventing information about the preexposure presentation of the target solution gaining access to LTM, then, with only generalized loss of

neophobia to the distractor involved, Group PD ought, at best, to have drunk as much lemon on the neophobia test as did Group P. That Group PD drank reliably more lemon than did Group P prompts the conclusion that Group PD experienced some loss of neophobia to the preexposed lemon solution in addition to generalized loss of neophobia to the coffee. In other words, the coffee distractor did not prevent information about the preexposure presentation of the lemon solution reaching LTM.

Closer examination of Wagner's (1976) model of stimulus processing suggests a way of reconciling the results of Experiment 1 with those obtained by Green and Parker (1975), providing one makes some assumptions regarding the relative degree of similarity between the distractor and the target solution in the two studies. Both retroactive and proactive interference of STM processing of events are recognized by the Wagner model. Because of the limited capacity of STM, the processing commanded by an unexpected event may disrupt processing of immediately preceding events in STM. At the same time, the amount of processing a stimulus commands on entry to STM is subject to proactive interference from items already present in STM. The greater the similarity between an incoming stimulus and the stimuli already present in STM, the less processing the incoming stimulus will attract and the less its ability therefore to retroactively interfere with processing of items already present in STM.

The model predicts, therefore, that a distractor that is dissimilar to a target solution will suffer less proactive interference from that flavour than will a distractor that is similar to the preexposed target flavour. In the former case, therefore, the processing accorded to the distractor may be sufficient to disrupt STM processing of the preceding target solution, thereby reducing the likelihood of information about the target flavour gaining access to LTM and thus interfering with habituation of neophobia to the target flavour.

In contrast, when the distractor and the target solution are similar, as may have been the case in Experiment 1, proactive interference from the target solution will reduce the amount of processing accorded to the distractor, thereby reducing its ability to retroactively disrupt the STM processing necessary for transfer of information about the target flavour to LTM. Loss of neophobia to the target solution as a result of its encoding in LTM might then be augmented by loss of neophobia to the distractor generalizing to the target solution to produce an enhanced habituation effect like that observed in Experiment 1.

2.5.3 Experiment 3

To test the possibility that the direction of a distractor effect is determined by the stimulus characteristics of the target solution and the distractor, Experiment 3 replicated the conditions of Experiment 1, but with a target solution assumed to be more dissimilar to the coffee distractor than was the lemon solution used in the previous experiments.

Both the lemon and the coffee solution possessed a strong odour, and while the lemon solution, at least to human senses, did not have any noticeable taste, the coffee tasted bitter. Rats readily discriminate sweet-tasting from bitter-tasting solutions (Nowlis, Frank & Pfaffmann, 1980). Thus, an odourless, sweet-tasting fluid (5% sucrose) was chosen as the target flavour in Experiment 3 on the assumption that the rat would perceive it to be less similar to the coffee distractor than was the lemon solution. Group NP, which was not preexposed to sucrose, was expected to drink less sucrose on the neophobia test than did Group P. The comparison of prime interest, however, is that of Group PD with Group P. If the prediction derived from Wagner's stimulus processing model is correct then one would expect Group PD to drink less sucrose on the neophobia test compared to that drunk by Group P.

Method

In all unspecified details, the procedure and apparatus were identical to those of Experiment 1.

Subjects

Twenty experimentally-naive female Lister rats (133-185 g), bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as rats in the previous experiments.

Procedure

The rats were placed on a 23.5 hour per day water deprivation schedule. On the test day, rats in Group P (n = 7) and Group PD (n = 7) were given a 5-min presentation of 5% (w/v) sucrose solution. This was followed immediately in the case of Group PD by a 5-min presentation of 1.25% (w/v) coffee solution, whereas rats in Group P were presented with an amount of water equivalent to the amount of coffee ingested by matched-weight control rats in Group PD. Rats in Group NP (n = 6) were allowed to drink an amount of water equivalent to the total amount of sucrose and coffee ingested by matched-weight control rats in Group PD. Six hours later, all rats were given a 10-min presentation of 5% sucrose solution.

Results

The 3 groups did not drink comparable amounts of sucrose on the neophobia test (see Figure 3). Group P drank 11.74 ml, Group PD drank 8.23 ml, and Group NP drank 7.70 ml. A oneway Anova indicated these differences were reliable ($F(2, 17) = 4.93$, $p < .05$). A posteriori comparisons with Duncan's Multiple Range Test (using an harmonic mean because of unequal N) indicated that Group PD and Group NP did not differ from one another in the amount of sucrose they drank ($p > .10$), but both these groups drank reliably less sucrose than did Group P ($p < .05$).

Discussion

Preexposure to the target solution again attenuated neophobia towards that solution on a subsequent occasion as is evident from the greater amount of sucrose drunk by Group P on the neophobia test compared to that drunk by Group NP. Of more interest, however, is the performance of Group PD, which drank significantly less sucrose than did Group P. In other words, presentation of a distractor disrupted the attenuation of neophobia resulting from preexposure to the sucrose. This result makes it unlikely that the enhanced attenuation of neophobia obtained by use of a distractor in Experiment 1 was the result of Group PD having drunk more novel fluid during preexposure than did Group P. Instead,

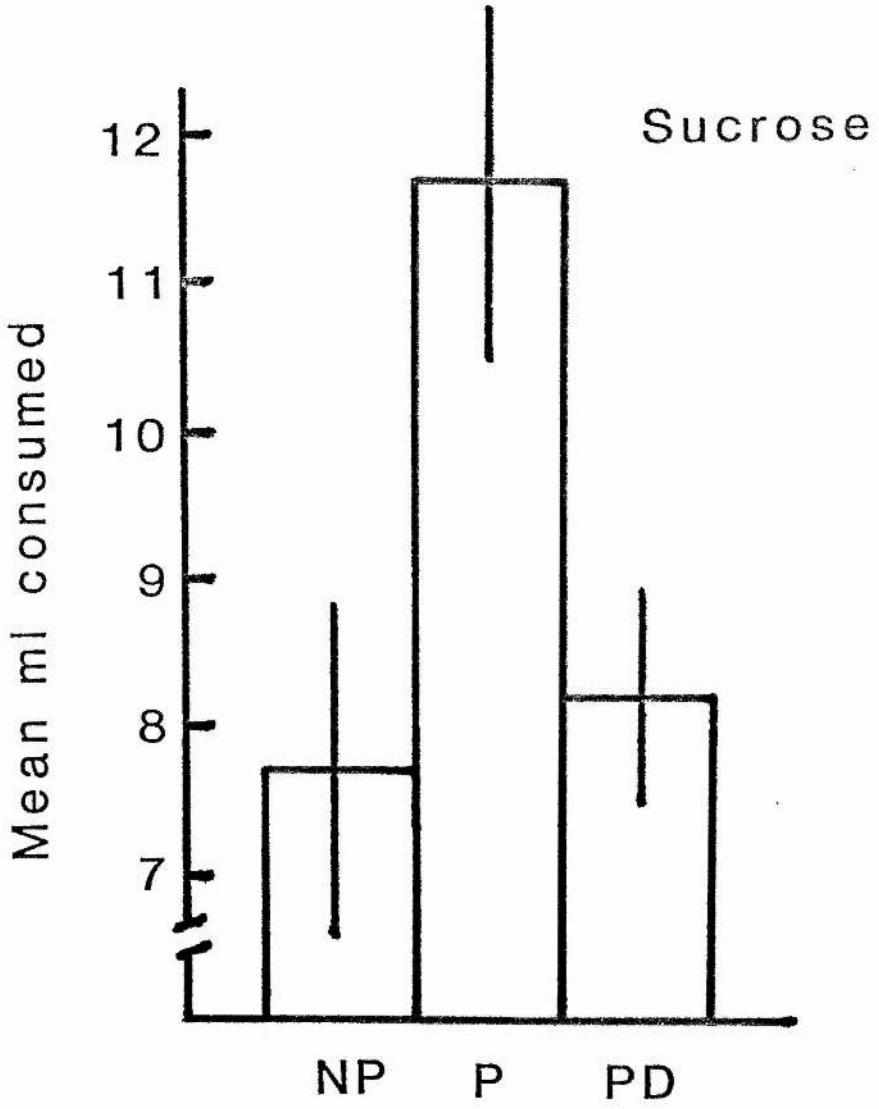

FIGURE 3. Mean consumption (ml) of target solution by groups P, PD and NP on the 10-min neophobia test in Experiment 3.

the performance of Group PD in Experiment 3 points to stimulus characteristics of the target solution interacting with those of the distractor to disrupt or enhance attenuation of neophobia towards a preexposed target solution.

2.5.4 Experiment 4

The results of Experiment 3 conformed nicely to those expected on the basis of Wagner's (1976) model of stimulus processing. An alternative hypothesis as to the cause of the bidirectional distractor effect observed in Experiment 1 and Experiment 3 must, however, be acknowledged: presentation of two solutions in close temporal proximity may produce a symmetrical change in the hedonic value of each solution as a consequence of its association with the other (c.f., Fanselow & Birk, 1982). In terms of the preceding experiments, therefore, if rats initially prefer sucrose to coffee, and coffee to lemon, then the attractiveness of the lemon solution may have been increased, and that of sucrose decreased, in the PD groups by virtue of their association with the coffee.

Fortunately, data were available from a pilot study in which two groups of rats, Group NP and Group P, were tested with a 1.25% coffee solution. As a preliminary check of the hedonic change hypothesis, Group NP of this pilot study was compared with Group NP of Experiment 1 and Group NP of

Experiment 3. If the hedonic change hypothesis is correct, one would expect to find that rats drank less lemon then coffee, and less coffee than sucrose (i.e., lemon < coffee < sucrose). In fact, the mean consumption of the 3 solutions was: lemon ($n = 8$) = 4.19 ml, coffee ($n = 8$) = 4.43 ml, and sucrose ($n = 6$) = 7.70 ml ($F(2, 19) = 9.94$, $p < .001$). Duncan's Multiple Range Test indicated that sucrose consumption was significantly greater than that of coffee or lemon ($p < .01$) which did not differ from one another.

Although this method of assessing the hedonic value of lemon, coffee and sucrose to the rat has certain limitations, the results of this comparison were of sufficient interest to suggest the desirability of an experiment specifically designed to test the hedonic change hypothesis. Accordingly, the conditions of Experiment 3 were replicated using coffee as the target solution and sucrose as the distractor. If the hedonic change hypothesis is correct, one would expect enhanced habituation of neophobia towards coffee because the coffee ought to become more attractive by virtue of its association with the more preferred sucrose solution. In contrast, the Wagner interference hypothesis would predict disruption of neophobia habituation similar to that observed in Experiment 3, since the order of presentation should not alter the degree to which the coffee and sucrose solution differ from one another (and hence the amount of proactive interference suffered by the distractor on entry to STM and the amount of

distractor-induced retroactive interference with processing of the target solution).

Method

In all unspecified details, the procedure and apparatus were identical to those of Experiment 1.

Subjects

Twenty-three experimentally-naive female Lister rats (124-184 g), bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as rats in previous experiments.

Procedure

The rats were placed on a 23.5 hour per day water deprivation schedule. On the test day, rats in Group P (n = 8) and in Group PD (n = 8) were given a 5-min presentation of 1.25% (w/v) coffee solution. This was followed immediately in the case of Group PD by a 5-min presentation of 5% (w/v) sucrose solution, while rats in Group P were presented with water equivalent in amount to the sucrose consumed by matched-weight control rats in Group PD. Rats in Group NP (n = 7) were allowed to drink an amount of water equivalent to the total amount of coffee and sucrose consumed by matched-weight control rats in Group PD. Six hours after the preexposure phase, all rats in each group were given a 10-min presentation of the coffee solution.

Results and Discussion

The amounts of coffee ingested on the 10-min neophobia test are shown in Figure 4. It is clear that the 3 groups did not drink equivalent amounts. Group NP drank 5.06 ml, Group PD drank 5.23 ml, and Group P drank 6.54 ml ($F(2, 20) = 5.19$, $p < .05$). Duncan's Multiple Range Test indicated that Group P drank significantly more coffee than did either Group PD or Group NP ($p < .05$) while these latter two groups did not differ from one another.

As in previous experiments, significant habituation of neophobia occurred as a result of preexposure to the target solution prior to the neophobia test (Group P versus Group NP). Of more interest, however, is the performance of Group PD. This group drank less coffee than did Group P and did not differ from Group NP which had no opportunity to drink coffee prior to the neophobia test. This is contrary to the prediction of the hedonic change hypothesis which expected Group PD to drink more coffee than Group P. The hedonic change hypothesis does not appear, therefore, to be an adequate explanation of the bidirectional distractor effect observed in Experiment 1 and Experiment 3. The disruption by the distractor of attenuated neophobia to the preexposed coffee solution in Experiment 4 was, however, exactly as predicted by the Wagner interference hypothesis.

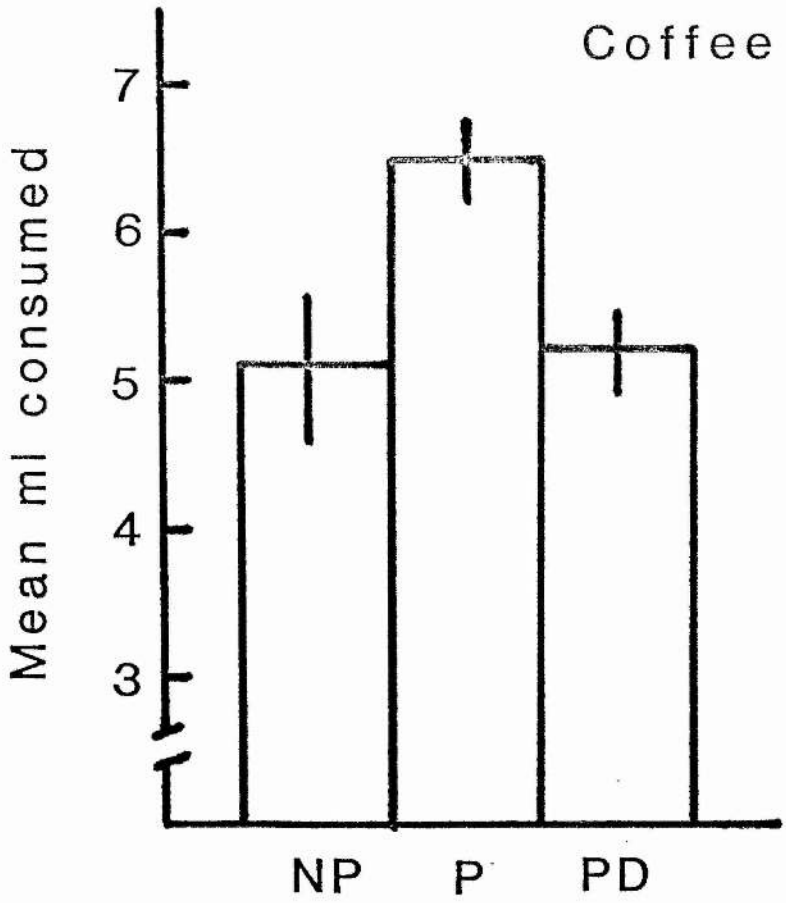

FIGURE 4. Mean consumption (ml) of target solution by groups P, PD and NP on the 10-min neophobia test in Experiment 4.

2.5.5 Experiment 5

Sucrose was chosen as the target solution in Experiment 3 because it was assumed to be less similar to the coffee distractor than was the lemon solution employed in Experiment 1. Since the explanation offered for the bidirectional distractor effect obtained in Experiment 1 and Experiment 3 focusses on assumed differences between the lemon and sucrose solutions in their degree of similarity to the coffee distractor, it was deemed prudent to obtain objective evidence in support of this assumption. Accordingly. one group of rats, Group E, was injected with Lithium Chloride after drinking coffee solution. Later the rats were offered the choice of drinking either lemon or sucrose solution. If lemon solution is indeed more similar to coffee than is sucrose, one would expect the conditioned taste aversion to coffee to generalize more to lemon than to sucrose. Group E should therefore exhibit a greater preference for sucrose than for lemon. A second group, Group C, was also injected with Lithium Chloride but without experiencing the coffee solution. Group C was later offered the same choice of drinking either lemon or sucrose solution. A comparison of Group C with Group E allows a conclusion as to whether any reduced preference for lemon over sucrose exhibited by Group E is dependent on prior experience of coffee paired with Lithium Chloride.

Method

Subjects

Sixteen experimentally-naive female Lister rats (138 - 198 gr), bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as rats in the previous experiments.

Procedure

All rats were placed on a 23.5 hour per day water deprivation schedule one week prior to conditioning. On the conditioning day, the rats were assigned to one of two groups (each of n = 8). Experimental rats (i.e., Group E) were given a 5-min presentation of novel 1.25% (w/v) coffee solution, followed immediately by a 15 ml/kg i.p. injection of .15M Lithium Chloride (LiCl). Control rats (i.e., Group C) were injected with LiCl after drinking water equivalent to the mean amount of coffee solution drunk by Group E. Following two recovery days in which rats were allowed to drink water in the test box for 10-min, followed by 20-min access to water in the home cage, each rat was given a two-bottle 10-min preference test involving 3% (v/v) lemon solution and 5% (w/v) sucrose solution. For half the animals in each group, the sucrose was initially presented on the left while for the remaining animals the sucrose was initially presented on the right. After 5-min the position of the drinking tubes was reversed. The next day, all rats

were given a single-bottle presentation of 1.25% coffee solution for 10-min.

Results and Discussion

Group E drank less coffee solution (1.33 ml) than did Group C (3.61 ml; see Figure 5). This difference was reliable ($t(14) = 4.55$, $p < .001$), and is consistent with Group E having acquired an aversion to the coffee solution as a result of experiencing the coffee paired with LiCl-induced toxicosis during the preexposure phase.

Group E and Group C did not differ in the absolute amount of lemon and sucrose combined that they drank (i.e., 7.60 ml and 7.80 ml, respectively) on the preference test ($t(14) = .26$). Although both groups drank more sucrose than lemon solution, the comparison of major interest is the relative magnitude of preference for lemon expressed by Group E and Group C (Lemon preference scores were calculated using the formula, $L/(L+S) \times 100$, where L = absolute intake of lemon, and S = absolute intake of sucrose on the two-bottle preference test.). Group E exhibited a smaller preference (4.6%) for lemon than that (10.3%) exhibited by Group C (see Figure 5). Although small, this difference was reliable ($t(14) = 2.47$, $p < .05$). Thus, the conditioned aversion to coffee generalized more to lemon than to sucrose. This supports the argument advanced earlier that the lemon solution is perceived by the rat to be more

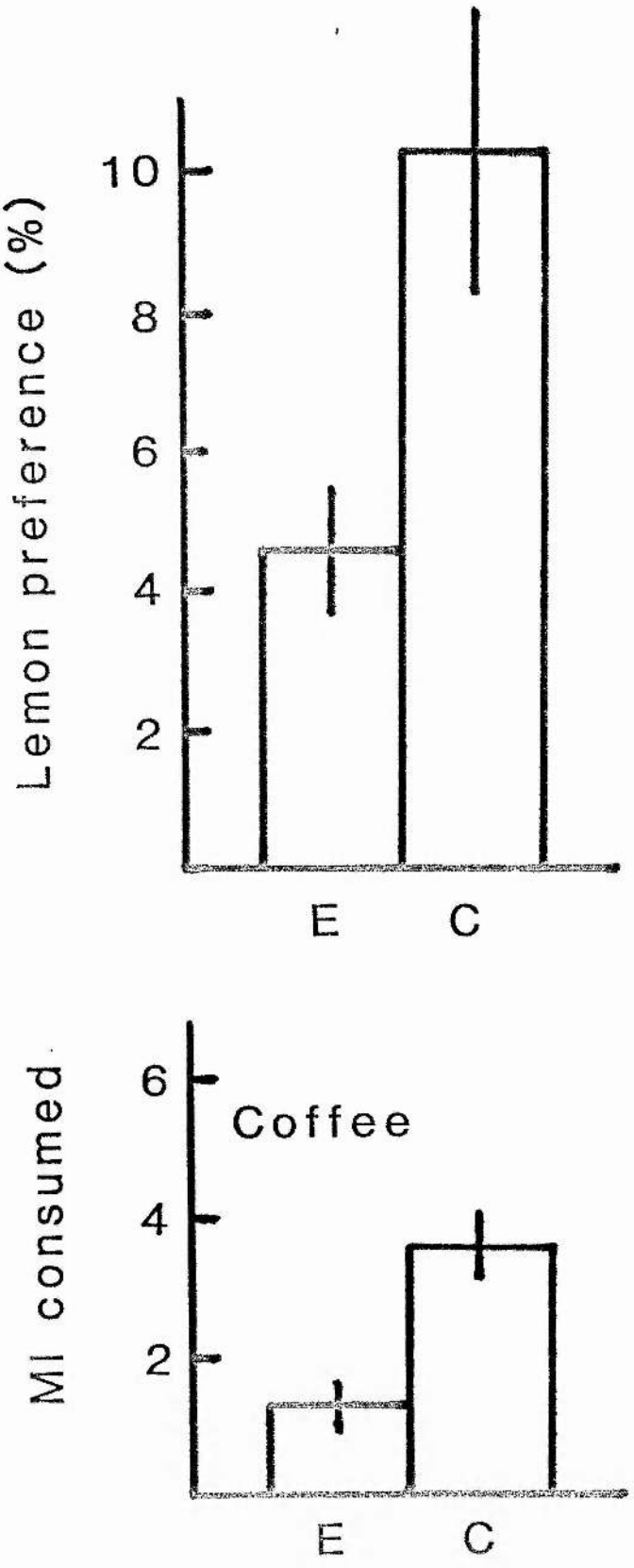

FIGURE 5. Results of Experiment 5. The lemon preference shown by experimental (E) and control (C) rats (calculated according to the formula, L/(L+S) x 100, where L = absolute intake of lemon, and S = absolute intake of sucrose) on the 10-min lemon vs. sucrose test is shown in the top panel of Fig. 5. In the lower panel is shown the mean consumption (ml) of coffee on the 10-min test of aversion to that solution.

similar to the coffee solution than is sucrose.

2.5.6 Experiments 6a and 6b

Experiments 6a and 6b each contained three groups, i.e, Group NP, Group P, and Group PD, treated in the same way as the corresponding groups of the same name in Experiment 1 and was designed to test whether the bidirectional distractor effect obtained in Experiment 1 and Experiment 3 is unique to the particular combinations of novel fluids used in those experiments. Three different solutions, whose degree of similarity to one another was known *a fortiori*, were used in Experiment 6a and 6b. These were selected from the table showing the relative similarity of 16 flavour solutions one to each other published by Parker and Revusky (1982), and were cider vinegar, hydrochloric acid (HCl), and evaporated milk. The vinegar served as the target solution in Experiment 6a, while the milk performed the same function in Experiment 6b. The distractor in both experiments was HCl.

Parker and Revusky (1982) demonstrated that an aversion conditioned to HCl generalized to vinegar, but not to milk, indicating that the rat perceived HCl to be similar to vinegar, but dissimilar to milk. If the direction of a distractor effect depends on the degree of similarity between target solution and distractor, as has been argued, one would expect to observe enhanced habituation of neophobia to vinegar in Experiment 6a, but disruption of

attenuated neophobia to the preexposed milk solution in Expt. 6b.

Method

In all unspecified details, the procedure and apparatus were identical to those of Experiment 1.

Subjects

Forty-eight experimentally-naive female Lister rats, bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as rats in the previous experiments. Twenty-four rats (132-187 g) were run in Experiment 6a and 24 rats (126-190 g) in Experiment 6b.

Procedure

Experiment 6a and 6b each contained 3 groups, viz., Group NP, Group P, and Group PD (each of n = 8). With the single exception that the target solution in Experiment 6a was 3% (v/v) cider vinegar, while in Experiment 6b the target solution was 50% (v/v) evaporated milk, the procedure in the two experiments was identical.

The rats were placed on a 23.5 hour per day water deprivation schedule and accustomed to drinking in the test box. On the test day, all rats in each group were given a 10-min presentation of the target solution (vinegar or milk).

Six hours prior to the 10-min neophobia test Group P and Group PD received a 5-min preexposure to the target solution (vinegar or milk). This was followed immediately by a 5-min presentation of 1.5% HCl to Group PD, while rats in Group P received instead water equivalent in amount to the mean amount of HCl drunk by rats in Group PD. Rats in Group NP drank only water during the preexposure phase; the amount drunk being equivalent to the mean combined amount of target solution (vinegar or milk) and HCl drunk by rats in Group PD.

Results

The amounts of the target solution drunk on the 10-min neophobia test are shown in Figure 6. The data from Experiment 6a are shown on the left of Fig. 6; the data from Experiment 6b are shown on the right.

In both experiment 6a and 6b, the groups did not drink comparable amounts of the target solution on the neophobia test (Fs (2, 21) = 11.04 and 19.94 respectively, $ps < .001$). As expected, when distractor and target solution were similar (Expt. 6a), Group PD drank more target solution (8.49 ml) than did Group P (7.13 ml), whereas when distractor and target solution were dissimilar (Expt. 6b), Group PD drank less target solution (6.26 ml) than did Group P (6.80 ml).

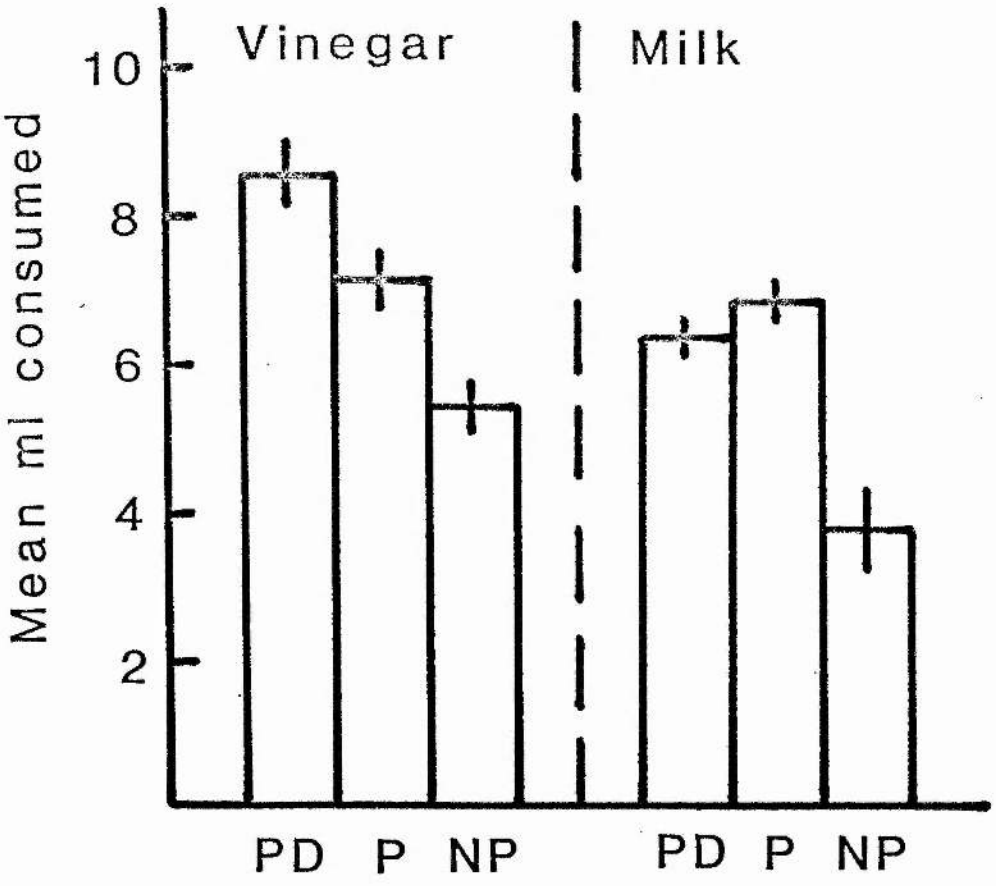

FIGURE 6. Mean consumption (ml) of target solution by groups P, PD and NP on the 10-min neophobia test in Experiment 6a (left panel) and in Experiment 6b (right panel).

Planned, non-orthogonal comparisons were analysed using the Bonferroni technique (Miller, 1966), i.e., to control for inflation of Type 1 error rates, the significance of any one comparison was assessed using the criterion of divided by the total number of comparisons of interest. A one-tailed test (with α = .05) was used because the direction of the difference between groups was specified a priori.

In Expt. 6a, planned comparisons confirmed that the amount of vinegar consumed during testing by Group P reliably exceeded the amount (5.39 ml) drunk by Group NP ($t(21) = 2.83$, $p < .01$) and indicated that the greater amount of vinegar consumed by Group PD, in comparison to that consumed by Group P, was marginally significant ($t(21) = 1.98$, $p = .06$).

In Expt. 6b, planned comparisons indicated that the amount of milk drunk during during testing by Group P reliably exceeded that drunk by Group NP ($t(21) = 5.35$, $p < .0001$). However, although the difference between Group PD and Group P was in the direction predicted, i.e., Group PD drank less milk than did Group P, this effect was not statistically significant ($t(21) = 1.68$, $p = .10$).

Discussion

The results of Expt. 6a and 6b, i.e., a distractor similar to a target solution tended to enhanced habituation to that solution, while the same distractor tended to disrupt habituation to a dissimilar target solution, indicate that the bidirectional distractor effect obtained in Expt. 1 and Expt. 3 is not unique to the particular combination of novel fluids employed in those experiments.

Although replicating the results of Expt. 1 and Expt. 3, the magnitude of difference between Group P and Group PD in the amount of target solution drunk during the 10-min neophobia test in Expt. 6a and 6b was not as great as the difference between the corresponding groups when lemon or sucrose was the target solution and coffee was the distractor. The reason is no doubt attributable to the apparently unpalatable nature of the HCl distractor. Rats in Group PD drank very little HCl (mean = 0.33 ml; range 0.1-0.5 ml) in Expt. 6a and 6b. Mean consumption of coffee distractor in Expt.1 and Expt. 3 was 2.01 ml (range = 0.2-5.7 ml). The loss of neophobia to HCl generalizable to the vinegar solution was probably less therefore than would have been the case if amount of HCl ingested had been greater. Similarly, the STM processing demanded by the distractor (and hence the degree of interference with habituation to the milk solution) was probably less than

would have been the case if amount of HCl drunk had been greater. However, to the extent that the performance of Group PD relative to that of Group P in Expt. 6a and 6b was in the direction predicted on the basis of prior knowledge of the relative similarity of both the vinegar and the milk solution to HCl, these results lend support to the important role assigned to stimulus similarity in determining whether a distractor enhances or disrupts attenuation of neophobia to a preexposed target solution.

2.5.7 Experiments 7a and 7b

Experiments 7a and 7b sought to extend further the range of flavour solutions over which one may observe a bidirectional distractor effect. By choosing a distractor more palatable than was the HCl employed in Expts. 6a and 6b, it was hoped to produce a distractor effect of greater magnitude than that observed in Expts. 6a and 6b.

Vinegar was chosen as the distractor in both Expt. 7a and 7b on the basis of pilot work that indicated that rats (n = 8) would drink 1.4 - 3.3 ml vinegar in a 5-min period compared to the 0.1 - 0.5 ml HCl drunk by rats in Group 6a and 6b. The target solution in Expt. 7a was grape-juice and in Expt. 7b saline. The grape-juice and saline were selected from the table of flavour relatedness published by Parker and Revusky (1982) which indicated that rats perceived vinegar to be similar to grape-juice but

dissimilar to saline. Enhanced habituation of neophobia to the target solution was anticipated in Expt. 7a; disruption of attenuated neophobia to the target solution was expected in Expt. 7b.

Method

In all unspecified details, the procedure and apparatus were identical to those of Expt. 1.

Subjects

Forty-eight experimentally-naive female Lister rats, bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as rats in preceding experiments. Twenty-four rats (136-194 g) were run in Expt. 7a and 24 rats (158-202 g) in Expt. 7b.

Procedure

The target solution in Expt. 7a was 3% (v/v) grape-juice. In Expt. 7b, the target solution was .09% (w/v) NaCl. The distractor in both Expt. 7a and 7b was 3% (v/v) cider vinegar. Expt. 7a and 7b each contained three groups, i.e., Group NP, Group P, and Group NP (each of n = 8). These were treated in exactly the same way as the corresponding groups of the same name in Expts. 6a and 6b.

Results

The amounts of the target solution drunk on the 10-min neophobia test are shown in Figure 7. The data from Expt. 7a are shown on the left of Fig. 7; the data from Expt. 7b are shown on the right.

The groups in Expt. 7a did not drink comparable amounts of the target solution on the neophobia test ($F(2, 21) = 14.95$, $p < .002$). Group PD drank 7.75 ml, and Group P drank 6.33 ml of grape-juice. Planned, non-orthogonal comparisons confirmed that the difference between Group PD and Group P was reliable ($t(21) = 2.24$, $p < .05$) and that Group P drank reliably more grape-juice than did Group NP which drank only 4.19 ml ($t(21) = 3.19$, $p < .01$).

In contrast, all three groups in Expt. 7b drank comparable amounts (means 8.9-9.9 ml) of saline solution during testing ($F(2, 20) = .43$). There was no evidence, therefore, that the saline elicited a neophobic response in rats.

Discussion

The results of Expt. 7a extend the range of novel fluids with which one may observe enhanced habituation to a target solution by presentation of a similar distractor in close temporal proximity to the target solution during a

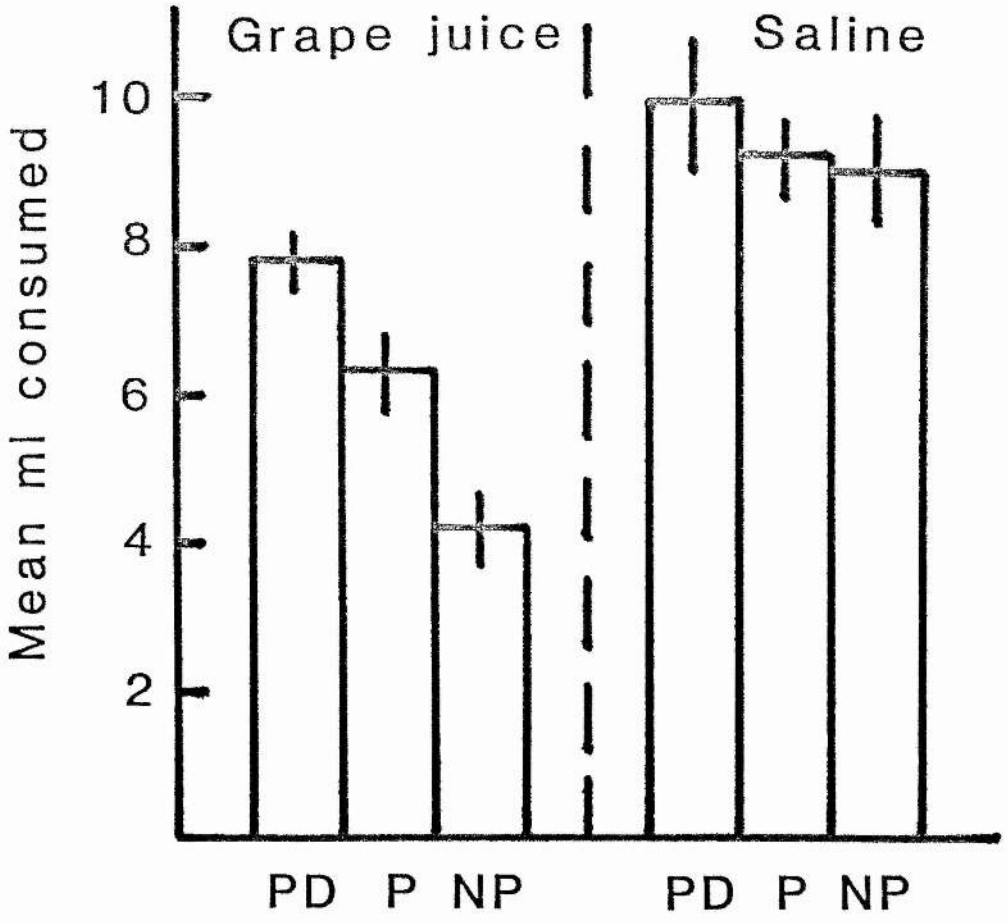

FIGURE 7. Mean consumption (ml) of target solution by groups P, PD and NP on the 10-min neophobia test in Experiment 7a (left panel) and in Experiment 7b (right panel).

preexposure phase and testify, thereby, to the robustness of the effect.

The failure to observe between-group differences in amount of saline drunk during the neophobia test in Expt. 7b may have resulted from a ceiling effect. A test session of longer duration than the 10-minutes employed in Expt. 7b might perhaps have produced evidence of attenuated neophobia resulting from prior experience of the target solution (i.e., Group P versus Group NP). Although possible, this is an unlikely explanation, however, of the uniform amount of saline drunk by groups in Expt. 7b. Carroll, Dinc, Levy, & Smith (1975) demonstrated that neophobia to a novel solution was best measured in a brief (10-min) single-bottle test than in a longer (60-min) single-bottle test: group differences in neophobia to a target solution in the Carroll et al (1975) study were produced by consistent differences in drinking rates which appeared early in the 10-min period.

A more likely explanation of the comparable amount of saline drunk during testing by rats in Expt. 7b is that the saline was not sufficiently novel to elicit neophobia. The rats' normal diet, dried food pellets, contains approx. 3% sodium (Wolf, McGovern & DiCara, 1974). Like other higher vertebrates, rats are well equipped to detect the taste of sodium: salt fibres form part of the primary taste modality (Denton, 1972). The rats in Expt. 7b may therefore have

recognized the taste of the saline solution as being similar to that of their laboratory chow and hence regarded the saline as "safe" (c.f., Kalat & Rozin, 1973) to drink.

Alternatively, saline may simply not elicit neophobia in rats. Salt is a necessary nutrient. Given the importance of ensuring an adequate intake of salt, it would appear biologically maladaptive to exhibit neophobia to novel salt solutions. Rather, one might expect instead rats to exhibit neophilia towards saline.

> "....sodium occurs in relatively pure form in nature and thus the capacity to locate, recognize and ingest it could carry significant survival advantage in sodium deficient ecological conditions" (Denton, 1972).

Nachman (1962), and Handal (1965) demonstrated an innate preference for sodium in sodium-deprived rats. However, sodium appetite does not depend on the presence of sodium need. Non-sodium deprived rats also drink large amounts of saline solution on the first occasion it is presented to them (Devenport, 1973; Fregly, Harper, & Radford, 1965; Wolf et al, 1974). Rats appear simply to have an innate preference for the sensory properties of mild saline solutions (Epstein, 1978).

There is an apparent contradiction between studies demonstrating rats have an innate preference for saline (Devenport, 1973; Fregly et al, 1965) and studies demonstrating a neophobic response of rats to saline solution (Braveman & Jervis, 1978; Miller & Holzman, 1981a, 1981b). On closer examination, however, the evidence of a neophobic response to saline by rats is not wholly convincing.

Using a between-groups design, Braveman and Jervis (1978) found that rats given eight 10-min presentations of isotonic saline drank more saline on a subsequent 10-min test than did rats that were given no prior exposure to saline. Miller and Holzman (1981a), using a within-group design, presented rats with ten 30-min exposures to isotonic saline and found that intake on Test 1 was less than the average intake of Tests 4-10. In a separate study, Miller and Holzman (1981b) demonstrated that rats given twelve 30-min presentations of isotonic saline drank more saline on a subsequent 30-min test than did rats that had no experience of the saline solution prior to the neophobia test.

That rats given extensive preexposure to saline solution drank more saline on a test than did rats encountering saline for the first time may not be evidence of a neophobic response to saline on the part of the

latter. Intake of a novel solution may increase as a function of experience of the ingesta even if that solution elicits no neophobia when it is first encountered. This may arise because the solution satisfies a physiological need, e.g., an initial attraction towards saline on the part of a sodium-deprived rat may be augmented by experience of the beneficial aftereffects of saline consumption (c.f., Smith, 1972), or because the hedonic value of the solution shifts in a positive direction with increasing experience of the solution (i.e., the rat may "acquire a taste" for the particular sensory properties of the target solution).

If a novel solution is consumed less readily when it is first encountered, compared to the amount of that solution which is ingested on a subsequent occasion, one cannot, therefore, conclude that the Day 1 intake indicates a neophobic response to that solution. Such a conclusion, to be valid, requires a demonstration that the Day 1 intake is less than would have been the case if a familiar solution had been presented instead of the novel solution. An appropriate comparison to determine whether or not a novel solution elicits neophobia or neophilia, when a single-bottle test is used (as was the case in the Braveman and Jervis study and in the two studies by Miller and Holzman), is to compare the amount ingested of that fluid when it is first encountered to the amount of water that is drunk during an equivalent time period. If water intake exceeds that of the novel solution, this would be evidence

of a neophobic response to the latter. If, however, intake of the novel solution were to exceed that of water, this would indicate a neophilic response to the novel solution.

In the Miller and Holzman (1981a) study, rats' intake of saline (16-25 ml) exceeded water intake of control animals (15-16 ml) on all test sessions, including the first. Drinking more of a novel solution on first encounter than the amount of water normally drunk during an equivalent time period would appear to indicate a tendency to approach (neophilia) rather than to avoid (i.e., neophobia towards) that novel solution.

Neither Braveman and Jervis (1978) nor Miller and Holzman (1981b) reported data on the amount of water that rats drank during a period equivalent in length to that of the saline test. One cannot readily assess, therefore, whether the rats in these studies exhibited neophilia or neophobia towards the saline when it was first encountered. Rats in the Miller and Holzman (1981b) study, however, were of the same strain as, and of comparable weight to, the rats used in the Miller and Holzman (1981a) study and the conditions of maintenance and the experimental procedure were identical in both studies. Since the amount of saline consumed on all trials by rats in the Miller and Holzman (1981b) study (20-25 ml) exceeded the amount of water that was drunk by control rats in the Miller and Holzman (1981a) study, this might be taken as suggestive evidence that

saline did not elicit a neophobic response from rats in the former study.

The neophobia of the laboratory-reared rat is of lesser magnitude than that of wild-reared rats (Mitchell, 1976) and it has commonly been found that the neophobia of the former to a novel flavour solution is significantly reduced by a single brief preexposure to that flavour (Domjan, 1976; Green & Parker, 1975; Siegel, 1974). In the Miller and Holzman (1981b) study, saline intake of experimental animals reached asymptote on the fourth 30-min exposure to saline. The difference between amount of saline drunk on Day 1 versus the amount consumed on Day 4, was not, however, significant. That three 30-min exposures to isotonic saline are not sufficient to increase saline intake of laboratory rats above that of rats encountering saline for the first time further argues caution in accepting the Miller and Holzman (1981b) data as evidence of a neophobic response to saline in rats.

2.5.8 Experiment 8

It has been argued that the bidirectional distractor effect obtained in preceding experiments is best understood in terms of the Wagner (1976) model of stimulus processing. Specifically, it has been suggested that a distractor such as coffee solution elicits less processing when preceded by a similar target solution (e.g., lemon) than is the case

when it is preceded by a dissimilar target solution (e.g., sucrose). Consequently, STM processing of lemon solution is subject to less retroactive interference from a coffee distractor than is sucrose. It was shown in Experiment 5 that the rat does perceive lemon to be more similar to coffee than is sucrose. Experiment 8 was designed to test the hypothesis that coffee suffers more proactive interference from a lemon solution than it does from sucrose.

If lemon does proactively interfere with processing of coffee more than does sucrose, then rats for whom preexposure to coffee is preceded by presentation of lemon solution (Group LC) should be less able to encode information about the coffee in LTM than are rats for whom preexposure to coffee is preceded by presentation of sucrose (Group SC). Group LC should thus drink less coffee on a subsequent test of neophobia to that flavour than do rats for whom preexposure to coffee is preceded by presentation of water (Group WC), whereas Group SC might be expected not to differ from Group WC in the amount of coffee drunk on the neophobia test.

Change in the hedonic value of the preexposed target solution as a result of its association with the distractor was earlier rejected as an explanation of the pattern of results obtained in Expt. 1 and Expt. 3. It is possible, however, that the hedonic value of the solution presented

second during the preexposure phase might undergo change as a result of association with the solution presented first. If that is the case, then unlike the Wagner model which expects no difference between Group SC and Group WC in the amount of coffee drunk on the neophobia test, the hedonic change hypothesis would predict Group SC to drink more coffee during testing than does Group WC because the attractiveness of the coffee solution to the former group is enhanced by virtue of its association with the more preferred sucrose solution. Both hypotheses, however, make the same prediction regarding the outcome of a comparison between Group LC and Group WC.

Method

In all unspecified details, the procedure and apparatus were identical to those of Experiment 1.

Subjects

Forty-seven experimentally-naive female Lister rats (141-198 g), bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as rats in the previous experiments.

Procedure

The rats were assigned to one of six groups; Group SC, Group LC, Group WC, Group SW, Group LW and Group WW. The two letters in the group designations represent the

solutions presented during the preexposure phase (i.e., C = Coffee, L = Lemon, S = Sucrose, W = Water) and the order of presentation. All groups contained eight rats, with the exception of Group SW which contained seven rats.

On the test day, rats were presented with 1.5 ml of 3% (v/v) lemon solution (Group LC and Group LW), 1.5 ml of 5% (w/v) sucrose solution (Group SC and Group SW) or 1.5 ml of distilled water (Group WC and Group WW). This was immediately followed by presentation of either 2.0 ml of 1.25% (w/v) coffee solution (Group LC, Group SC and Group WC) or 2.0 ml of distilled water (Group LW, Group SW and Group WW). Six hours after the preexposure phase, all six groups were given a 10-min presentation of the coffee solution.

Results and Discussion

The data from the 10-min neophobia test are shown in Figure 8. The groups did not drink comparable amounts of coffee. A oneway ANOVA indicated that the differences in amount drunk were reliable ($F(5, 41) = 9.34$, $p < .0001$).

A posteriori comparisons were made using Duncan's Multiple Range Test. As in previous experiments, preexposure to the target flavour attenuated neophobia to that flavour on a subsequent test, as is evident from the greater amount of coffee (8.15 ml) drunk by Group WC compared to that

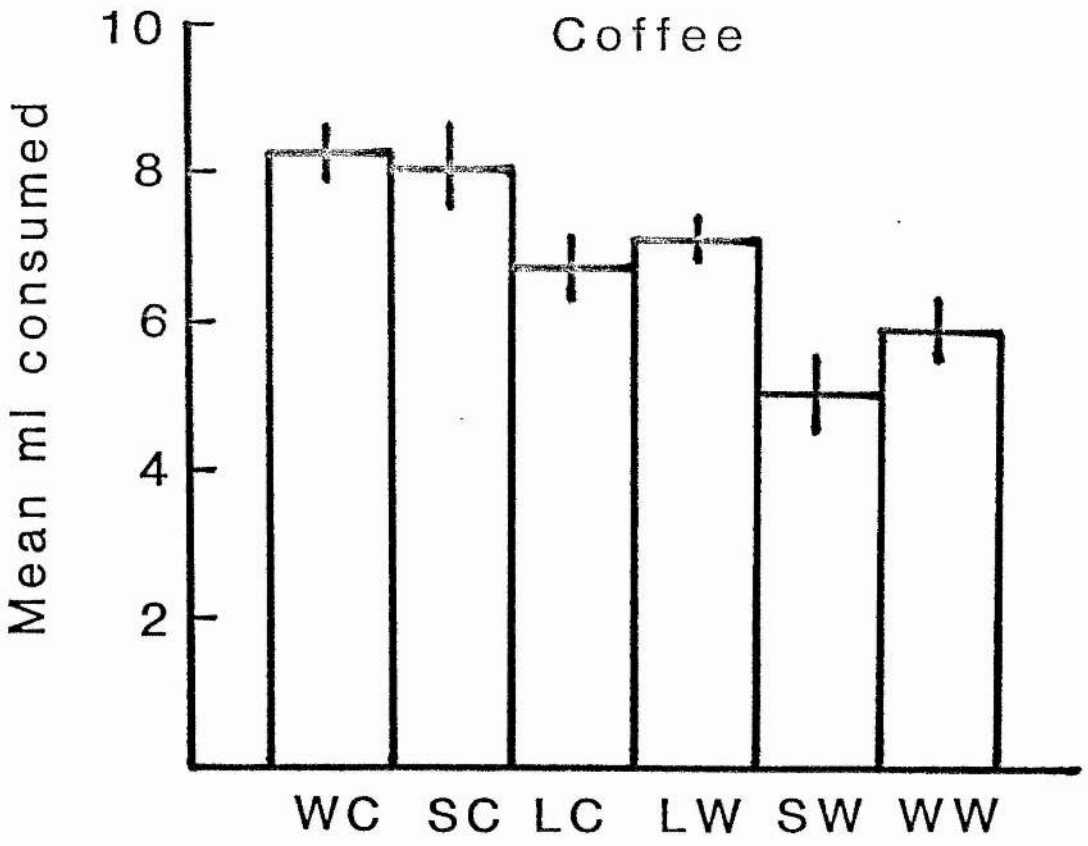

FIGURE 8. Mean consumption (ml) of target solution on the 10-min neophobia test in Experiment 8.

(i.e., 5.90 ml) drunk by Group WW ($p < .01$). This attenuation of neophobia to coffee was largely dependent on prior experience of the coffee solution. Rats preexposed to sucrose solution (i.e., Group SW) drank significantly less coffee (5.01 ml) on the subsequent test than did Group WC ($p < .01$) and did not differ in amount drunk from Group WW which had no experience of novel flavour solutions prior to testing with coffee. By contrast, rats preexposed to the lemon solution (i.e., Group LW) drank more coffee (7.13 ml) than did either Group WW or Group SW (ps $< .01$). This provides further evidence that a 3% lemon solution is perceived by rats to be more similar to a 1.25% coffee solution than is a 5% sucrose solution.

The comparisons of major interest, however, are those involving Group WC, Group SC, and Group LC. Although all 3 groups drank the same amount of coffee solution during preexposure, they did not drink equivalent amounts of coffee on the neophobia test. Group WC and Group SC drank comparable amounts of coffee (8.15 ml and 8.10 ml, respectively), but Group LC drank reliably less (6.65 ml) than either Group WC or Group SC (ps $< .05$). The comparable amount of coffee drunk during testing by Group WC and Group SC is contrary to the expectation of the hedonic change hypothesis, but consistent with that of the Wagner model, and would appear to indicate that the sucrose solution was ineffective in preventing information about the preexposed coffee solution being encoded in LTM. By contrast,

preceding the coffee solution by lemon during the preexposure phase appeared to reduce the amount of information about the preexposed coffee flavour that was encoded in LTM. This is evident from the greater degree of neophobia exhibited by Group LC towards the coffee during testing compared to that shown by Group WC and Group SC.

These results confirm the hypothesis that coffee suffers more proactive interference from lemon than from sucrose. In fact, since Group LC did not differ from Group LW in the amount of coffee drunk on the neophobia test, it would appear that, under the conditions of this experiment, the lemon may have completely prevented processing of the preexposed coffee solution in STM. This should not, however, be universally true. The extent to which coffee suffers proactive interference from the lemon might be expected to vary as a function of the relative amounts of lemon and coffee rats are allowed to drink during the preexposure phase.

A less interesting explanation of the data obtained in Expt. 8 is that, to the rat, coffee presented immediately after drinking lemon (but not after drinking sucrose) may taste different from the taste of coffee presented alone. The relative amount of coffee consumed during testing by Group SC and Group LC, therefore, might be the result of differential stimulus generalization decrement between the conditions of preexposure and testing.

2.5.9 Experiment 9

Experiment 9 sought to replicate the results of Experiment 8, viz., that the solution presented second during preexposure suffers more proactive interference from the solution presented first if the two solutions are similar to one another than is the case when the two solutions are dissimilar, using flavour solutions different from those used in Expt. 8. Accordingly, the target solution used in Expt. 9 was HCl, and the two distractor solutions were cider vinegar and evaporated milk. Since HCl is perceived by the rat to be more similar to cider vinegar than it is to evaporated milk (Parker & Revusky, 1982), it was expected that rats for whom preexposure to HCl was preceded by presentation of cider vinegar would exhibit more neophobia towards the HCl on a subsequent test than would rats for whom preexposure to HCl was preceded by presentation of evaporated milk. In other words, cider vinegar was expected to disrupt STM processing of the preexposed HCl more than did evaporated milk.

Method

In all unspecified details, the procedure and apparatus were identical to those of Expt. 1.

Subjects

Twenty-three experimentally-naive female Lister rats (138-186 g), bred in the Psychology Dept., University of St. andrews, were housed and maintained in the same way as were rats in preceding experiments.

Procedure

The rats were assigned to one of four groups; Group MH, Group VH, Group WH and Group WW. The two letters in the group designations represent the solutions presented during the preexposure phase (i.e., H = Hydrochloric acid, M = Milk, V = Vinegar, W = Water) and the order of presentation. All groups contained six rats, with the exception of Group WW, which contained five.

On the test day, rats were presented with 0.5 ml of distilled water (Group WW and Group WH); 0.5 ml of 3% (v/v) cider vinegar (Group VH); or 0.5 ml of 50% (v/v) evaporated milk (Group MH). This was followed immediately by a 0.5 ml presentation of 1.5% (v/v) HCl (Group WH, Group MH and Group VH) or a 0.5 ml presentation of water (Group WW). Six hours later, all rats in each group received a 10-min presentation

of HCl.

Results and Discussion

The amounts of HCl drunk on the 10-min neophobia test are shown in Fig. 9. A oneway ANOVA confirmed that the four groups did not drink comparable amounts of HCl ($F(3, 19) = 7.91$, $p < .01$). A posteriori comparisons with DMRT indicated that there was a reduction in neophobia as a result of preexposure to HCl prior to testing; Group WH drank significantly more HCl (i.e., 1.25 ml) than the amount (0.56 ml) consumed by Group WW ($p < .01$). The difference in the amount of HCl consumed by Group VH and Group MH, although in the direction expected (0.85 ml and 1.05 ml, respectively), was not statistically significant ($p > .10$). The comparisons of major interest, however, are those of Group WH with Group MH, and Group WH with Group VH. Group MH and Group WH did not differ in amount of HCl ingested during the 10-min test ($p > .10$), but Group VH drank significantly less HCl on the neophobia test than did Group WH ($p < .05$) and did not, in fact, differ from Group WW ($p > .05$). The results of this experiment are therefore in line with those found in Expt. 8, i.e., the attenuation of neophobia to a preexposed target solution was reliably disrupted if preexposure to the target solution was immediately preceded by presentation of a solution similar to the target solution, but not if it was preceded by presentation of a dissimilar solution.

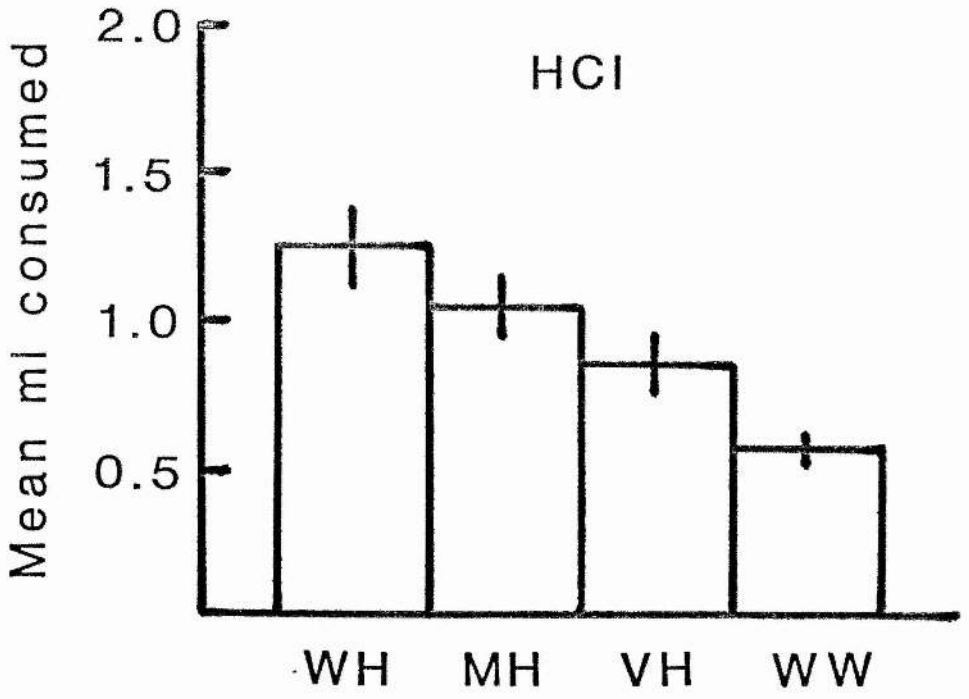

FIGURE 9. Mean consumption (ml) of target solution on the 10-min neophobia test in Experiment 9.

2.6 Summary

The data gathered thus far indicate that the effect of presenting a distractor during the interval between preexposure to a novel target flavour and a subsequent test of neophobia to that flavour is not invariant. The distractor may enhance (Expt. 1) or disrupt (Expt. 3) habituation of neophobia to a target flavour. This bidirectional effect is not the result of distractor-induced change in the hedonic value of the target flavour (Expt. 4). Rather, the degree of similarity between distractor and target flavour appears to be important (Expt. 5). When distractor and target flavour are similar enhanced habituation to the target flavour is observed. In contrast, when distractor and target flavour are dissimilar, habituation to the target flavour is disrupted. This pattern of results is not unique to a particular combination of flavour solutions (Expts. 6a and 6b).

The data are compatible with Wagner's (1976) stimulus processing model which assumes that the amount of processing a distractor receives on entering STM depends on the identity of the stimuli already occupying STM. When a distractor is preceded by a similar target flavour it will elicit less processing in STM as a result of proactive interference from the target flavour than will be the case when preceded by a dissimilar target flavour (c.f., Expts.

8 and 9). As a consequence of proactive interference, a distractor will thus be less likely to deny the limited-processing capacity of STM to a similar target flavour than will be the case when the distractor and target flavour are dissimilar. Information about the preexposed target flavour will thus be more likely to gain access to LTM in the former case than in the latter. In addition, any loss of neophobia to the distractor may generalize to a similar target flavour and augment the loss of neophobia resulting from encoding of information about the target flavour itself in LTM.

Whilst it has been shown that a distractor may either enhance or disrupt AN to a target solution; the direction of effect apparently depending upon the relative similarity of the two solutions and whether the distractor immediately precedes or immediately follows the target solution during the preexposure phase, encouraging thereby the differential memorial processing account offerred of the data, a note of caution must be sounded. Firstly, conclusions as to the relative degree of similarity of the solutions used in the above experiments were based on the results of taste aversion experiments in which the extent to which an aversion established to one solution generalized to other non-poisoned solutions was taken to indicate the degree to which these solutions are perceived by the rat to be similar to one another (Expt. 5 this thesis; Parker & Revusky, 1982). It is possible, however, that the relative

similarity of one solution to another, as perceived by the rat, is not the same across all situations. Although Expt. 8 above, using generalization of AN as the response measure, yielded results regarding the perceived similarity or dissimilarity, one to another, of the solutions used in Expts. 1-4 that were identical to those obtained using a generalization of conditioned aversion procedure, no comparable evidence was provided to show that the relative similarity of the solutions used in Expts. 6a-7b was perceived by the rat to be the same regardless of whether generalization of a conditioned aversion or generalization of AN was the response measure.

Secondly, the demonstration of either enhanced or diminished AN to a preexposed target solution by a distractor in the above experiments is confounded with the choice of target solution, i.e., the target solution was varied across experiments while holding the distractor constant (e.g., lemon-coffee in Expt. 1; sucrose-coffee in Expt. 3). The hypothesis that it is the relative similarity of the target solution and the distractor (rather than some as yet unidentified factor) that is important in determining the pattern of results obtained above would undoubtedly by strengthened, therefore, if a complimentary series of studies (in which the target solution is held constant while varying the distractor) was able to demonstrate that AN to the <u>same</u> target solution may either be enhanced or disrupted by presentation of similar or

dissimilar distractor solutions.

3 LATENT INHIBITION (LI) OF CTA

Diminution of the UR is not the only consequence of repeated presentation of a target stimulus. If a preexposed stimulus, A, is later paired with a novel stimulus, B, formation of an association between A and B is retarded relative to that which would have occurred if A had been novel when paired with B. The decrement in associative learning following preexposure to a CS is termed latent inhibition (for review see Lubow, 1973).

3.1 LI and habituation: common causal mechanism?

According to the Wagner (1976) model, latent inhibition arises because preexposure to the target stimulus, A, results in A being primed in STM prior to its presentation in a conditioning relationship to B. As a consequence of this priming effect, A does not elicit the processing necessary to promote an association with B. Latent inhibition, therefore, shares with habituation the same underlying causal mechanism.

3.2 Some experimental predictions

The merit of regarding latent inhibition and habituation as manifestations of a common process would be strengthened by demonstration that both are affected similarly by identical parametric manipulations. One

implication of the Wagner (1976) distinction between self- and retrieval-generated priming of STM is the possibility of separable short- and long-term stimulus preexposure effects related to the temporal interval separating preexposure and the conditioning or test presentation of the target stimulus, i.e., inter-stimulus interval (ISI). With a short ISI, the decrement in processing the second presentation of the target stimulus may be attributed to self-generated priming. In contrast, with a comparatively long ISI the decrement in processing the second presentation of the target stimulus must be attributed to retrieval-generated priming.

The Wagner model predicts that the proximal and the remote preexposure effect will be differently affected by the same variables. The notion of self-generated priming, together with the notion that items progressively decay from STM over time (c.f., Krane & Robertson, 1982; Roberts & Grant, 1976), the rate of decay being inversely related to stimulus intensity (Krane & Wagner, 1975), implies that the proximal preexposure effect should be directly related to stimulus intensity and inversely related to ISI. In other words, at any given ISI a more intense or longer duration preexposure presentation of the target stimulus will decay from STM more slowly than preexposure to a target stimulus of lesser intensity or shorter duration. Consequently, there will be a larger priming-induced decrement in STM processing of the conditioning or test presentation of the

target stimulus in the former than in the latter condition. Similarly, at any given intensity or duration of a target stimulus presented during preexposure, the shorter the ISI, then the less will information about the preexposure presentation of the target stimulus have decayed from STM by the time of the CS-US trial or habituation test and the greater will be the priming-induced decrement in STM processing of the conditioning or test presentation of the target flavour.

A further expectation of the Wagner model with regard to proximal stimulus preexposure effects, is that such effects, to the extent that they are the consequence of self-generated priming of STM, should be independent of context, i.e., learning of an association between A and B should be equally retarded whether preexposure to A occurs in a context different from or the same as that in which conditioning takes place. Likewise, habituation of the UR to A should be unaffected by any change of context between preexposure to A and testing.

To iterate, the decrement in both associative learning and habituation following a proximal preexposed stimulus should be, i) directly related to the intensity or duration of the preexposed target stimulus, ii) inversely related to the interval separating preexposure from the conditioning or test presentation of the target stimulus (i.e., the ISI), and iii) context-independent.

In contrast, while the remote preexposure effect may also be directly related to intensity or duration of the preexposure presentation of the target stimulus (a more intense or longer lasting stimulus might promote a stronger association with accompanying contextual cues), it should be directly (if only weakly), and not inversely, related to ISI. This is because the greater the ISI, the less opportunity there will be for the conditioning presentation of the target stimulus to disrupt the STM processing necessary to associate the preexposure presentation of the target stimulus with contextual cues. Additionally, the remote preexposure effect, unlike that of the proximal, should be context-dependent. Since the remote stimulus preexposure effect results from STM being primed with information about the target stimulus retrieved from LTM by the action of cues associated with the preexposure presentation of the target stimulus, changing the cues present on the conditioning trial or habituation test from those that were present during preexposure should prevent or reduce any retrieval-generated priming of STM.

3.3 Review of the evidence

Rats injected with lithium chloride (LiCl) after consuming a novel flavour subsequently avoid ingesting that flavour solution, i.e., pairing LiCl-induced toxicosis (US) with a novel flavour (CS) conditions an aversion to the CS.

The strength of this aversion is reduced, however, if the flavour (CS) is experienced prior to the CS-US pairing (i.e., latent inhibition). Throughout the discussion that follows, the studies of latent inhibition referred to employed a conditioned taste aversion procedure.

Proximal and remote preexposure effects have been observed for both latent inhibition (Best & Gemberling, 1977; Domjan & Bowman, 1974; Kalat & Rozin, 1971, 1973; Siegel, 1974; Westbrook, Bond, & Feyer, 1981) and habituation (Bond & Westbrook, 1982; Davis, 1970).

The proximal preexposure effect is directly related to the intensity of the preexposed target stimulus for both latent inhibition (Rudy & Cheatle, 1978) and habituation (Davis & Wagner, 1968) and is inversely related to the ISI in both latent inhibition (Best & Gemberling, 1977) and habituation (Davis, 1970; Terry, 1979; Wilson & Groves, 1973). In addition, the proximal preexposure effect is not context-dependent in latent inhibition (Westbrook, et al, 1981; Westbrook, Provost & Homewood, 1982). I do not know, however, of any evidence as to whether or not the proximal preexposure effect in a habituation paradigm is context-specific.

In contrast to the proximal preexposure effect, the remote preexposure effect is context-dependent for both latent inhibition and habituation. Changing the context between preexposure and the CS-US trial lessens the retardation of conditioning that otherwise results from preexposure to the CS (Rudy, Rosenberg, & Sandell, 1977; Westbrook et al, 1981). Similarly, changing the context between preexposure to a target stimulus and testing disrupts habituation to the target stimulus whether that target stimulus be food (Chance & Mead, 1955; Mitchell, Scott & Williams, 1973), a drug (Advokat, 1980; Crowell, Hinson, & Siegel, 1981; Le, Poulos, & Cappell, 1979; Mansfield & Cunningham, 1980; Siegel, 1976, 1978; Siegel, Hinson, & Krank, 1978, 1979) or a maze (Terry, 1979), but see Leaton (1974) for a failure to obtain evidence that long-term habituation of the rat's startle-response to iterated acoustic stimuli is context-specific).

The remote preexposure effect is directly related to the ISI in latent inhibition (Kalat & Rozin, 1971) and in habituation (Davis, 1970; File, 1973). In addition, the magnitude of the remote preexposure effect appears to be directly related to the duration of the preexposed target stimulus in both latent inhibition and habituation. For example, Westbrook et al (1981; Expt. 3) presented rats with a 5-min odour CS followed by LiCl and found that the resultant odour aversion was weaker if the conditioning

conditioning episode had been preceded 24 hours earlier by a 5-min rather than a 2-min presentation of the to-be-conditioned CS. Parker (1976) allowed rats 1, 2, 5, 15 or 30-min access to a novel 0.02% saccharin solution and found that attenuation of neophobia to that solution on a test 24 hours later was positively related to the duration of initial exposure. A similar positive relationship between duration of initial exposure to a novel solution and subsequently demonstrated attenuation of neophobia was reported by Best, Domjan and Haskins (1978) who gave rats either 20-min or 120-min access to novel 1.0% saccharin and tested for neophobia 48 hours later.

This limited review indicates sufficient similarity between studies of latent inhibition and habituation to a preexposed target stimulus in terms of response to identical parametric manipulations to encourage acceptance of the Wagnerian hypothesis of a single causal mechanism underlying both phenomena. That being the case, Expts. 10a and 10b sought to determine whether a bidirectional distractor effect similar to that obtained with an habituation procedure might also be found in a latent inhibition design.

3.4 PRESENT STUDIES

3.4.1 Experiments 10a and 10b

Previous flavour aversion studies that investigated the effect of interpolating a distractor flavour in the interval separating preexposure and conditioning presentations of a target flavour obtained mixed results. Best, Gemberling, and Johnson (1979) reported disruption of latent inhibition when the target flavour was a nominal 3% vinegar solution and the distractor was a nominal 3% vanilla solution. In contrast, Westbrook et al (1982), although obtaining reliable latent inhibition to a preexposed saline or sucrose target solution, were unable to disrupt this effect by presentation of a sucrose or saline (respectively) distractor.

In attempting to reconcile their own results with those of Best et al (1979), Westbrook et al speculated that the short (2-min) flavour preexposure duration in their study (Best et al (1979) employed a 5-min flavour preexposure duration) may have been of insufficient length to promote an association between the target flavour and accompanying contextual cues. The opportunity for the distractor to disrupt retrieval-generated priming of the target flavour in STM might not therefore have existed. Similarly, the short 2-min preexposure to the target flavour and the distractor

may not have been of sufficient duration to overload the limited processing capacity of STM thus explaining why self-generated priming of the target flavour in STM was not disrupted by the distractor. It was hoped that the 5-min presentation of distractor and target flavour during the preexposure phase of Expts. 10a and 10b would be sufficiently long to yield evidence of a distractor effect. The 5-min duration of flavour exposure was chosen to permit comparison of the results of Expts. 10a and 10b with those of preceding experiments in which the same novel solutions were used in a neophobia design and also with those of Best et al (1979).

In Expts. 10a and 10b, one group of rats, Group NP, received a target solution (sucrose in Expt. 10a; lemon in Expt. 10b) paired with LiCl. Two other groups, Group P and Group PD, were given a brief preexposure to the target solution 6 hours prior to its pairing with LiCl. One group, Group PD, received a brief presentation of a distractor flavour (coffee solution in both Expt. 10a and 10b) immediately after preexposure to the target solution. After allowing recovery from the ill-effects of the LiCl, the strength of aversion conditioned to the target solution was assessed by presenting all rats with the target solution alone. One would expect Group P to drink more of (i.e., exhibit less of an aversion to) the target solution than Group NP, i.e., a latent inhibition effect. More interestingly, given the results of the preceding

experiments on habituation of neophobia to lemon and sucrose with a coffee distractor, one might expect to obtain disruption of latent inhibition when sucrose is the target solution (Expt. 10a), but enhanced latent inhibition when lemon is the target solution (Expt. 10b), i.e., Group PD should acquire a stronger aversion to the target solution than does Group P in Expt. 10a, but a weaker aversion to the target solution than does Group P in Expt. 10b.

Method

In all unspecified details, the procedure and apparatus were identical to those of Experiment 1.

Subjects

Forty-eight experimentally-naive female Lister rats, bred in the Psychology Dept., University of St. Andrews, were housed and maintained in the same way as were rats in the preceding experiments. Twenty-four rats (162-233 g) were run in Expt. 10a; and 24 rats (156-200 g) in Expt. 10b.

Procedure

Expts. 10a and 10b each contained three groups, i.e., Group NP, Group P, and Group PD (each of N = 8). The target solution in Expt. 10a was 5% (w/v) sucrose; in Expt.10b, the target solution was 3% (v/v) lemon. A 20 ml/kg i.p. injection of .15M LiCl was employed as the US in Expt.

10a. A pilot study with lemon as the target solution and a 20 ml/kg injection of .15M LiCl obtained no evidence of a latent inhibition effect. The dosage of LiCl was thus reduced from 20 ml/kg to 10 ml/kg in Expt. 10b. Apart from these exceptions, the procedure in Expts. 10a and 10b was identical.

The rats were placed on a 23.5 hour per day water deprivation schedule and accustomed to drinking in the test box. Commencing at 1400 h on Day 1, the conditioning day, rats in Group NP, Group P, and Group PD were allowed to drink 5.0 ml of sucrose (Expt. 10a) or 3.0 ml of lemon (Expt. 10b) solution followed 30-min later by administration of the LiCl (20 ml/kg dose in Expt. 10a; 10 ml/kg dose in Expt.10b). Six hours prior to the paired presentation of the target solution and LiCl, rats in Group P and in Group PD were given a 5-min preconditioning presentation of sucrose (Expt. 10a) or lemon (Expt. 10b). In both experiments, rats in Group PD received a 5-min presentation of a 1.25% (w/v) coffee solution presented immediately after the preconditioning presentation of the target solution. Rats in Group P were presented with water immediately after the preconditioning exposure to the target solution; the amount of water presented being equivalent to the mean amount of coffee solution consumed by rats in Group PD. Rats in Group Np were allowed to drink water equivalent to the mean amount of target flavour and coffee solution consumed by rats in Group PD.

Commencing at 1400 h on Day 2 and Day 3, all rats were given a 10-min presentation of water in the test box to allow recovery of baseline levels of fluid intake. This was followed by a 20-min presentation of water in the home cage.

Testing took place on Days 4-6. On Day 4 and Day 5, Group NP, Group P, and Group PD were given a 10-min presentation of sucrose (Expt. 10a) or lemon (Expt. 10b). On Day 6, all rats were given a 10-min presentation of coffee solution. All test sessions commenced at 1400 h.

Results

The data for consumption of the target solution on the two 10-min tests are shown in Figure 10. The data from Expt.10a are shown on the left of fig. 10; the data from Expt. 10b are shown on the right.

In Expt. 10a, Group P and Group PD drank comparable amounts of sucrose on both Test 1 (6.49 ml and 6.49 ml, respectively) and on Test 2 (9.91 ml and 10.38 ml, respectively). In contrast, Group NP drank only 0.95 ml sucrose solution on Test 1 and only 4.06 ml on Test 2. A 3 x 2 ANOVA performed on the data from Expt.10a indicated that there was a significant effect of Group ($F(2, 21) = 38.99$, $p < .0001$) and of Test ($F(1, 21) = 145.21$, $p < .0001$).

There was, however, no Group x Test interaction ($F(2, 21) = 0.61$). Consequently, the group data were collapsed across Tests and a posteriori comparisons with the DMRT confirmed that both Group P and Group PD, while not differing from one another, drank significantly more sucrose than did Group NP ($p < .01$).

The data from the 10-min coffee test in Expt. 10a are shown on the left of Figure 11. A oneway ANOVA indicated that there was no significant difference in coffee consumption (means 4.65-6.10 ml) of the 3 groups ($F(2, 21) = 2.63$, $p > .05$). There was thus no evidence to suggest that any aversion was conditioned to coffee in Group PD. It should be noted, however, that any aversion to coffee in Group PD may have been masked by a neophobic response to coffee by Groups P and NP, both of which experienced coffee for the first time during testing. Inclusion of a control group that received the distractor immediately after preexposure to the target solution and then had the target solution paired with injection of NaCl on the conditioning trial would have allowed a more confident conclusion as to whether or not an aversion was conditioned to coffee in Group PD.

Expt. 10b revealed a pattern similar to that of Expt. 10a. Group P and Group PD drank more lemon solution on both Test 1 (4.23 ml and 3.20 ml, respectively) and on Test 2 (6.75 ml and 5.61 ml, respectively) than did Group NP (0.99

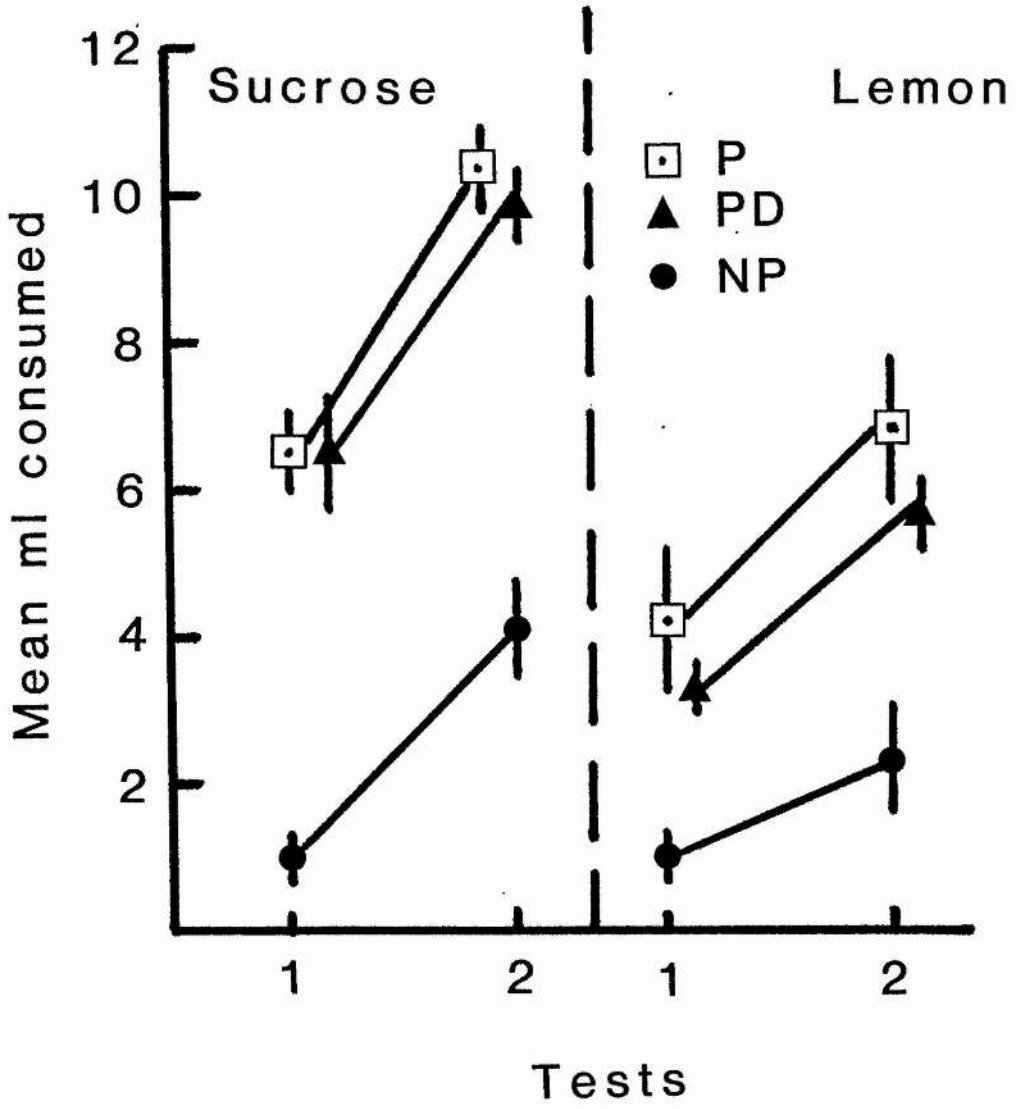

FIGURE 10. Mean consumption (ml) of target solution by groups P, PD and NP on the two 10-min tests of latent inhibition in Experiment 10a (left panel) and in Experiment 10b (right panel).

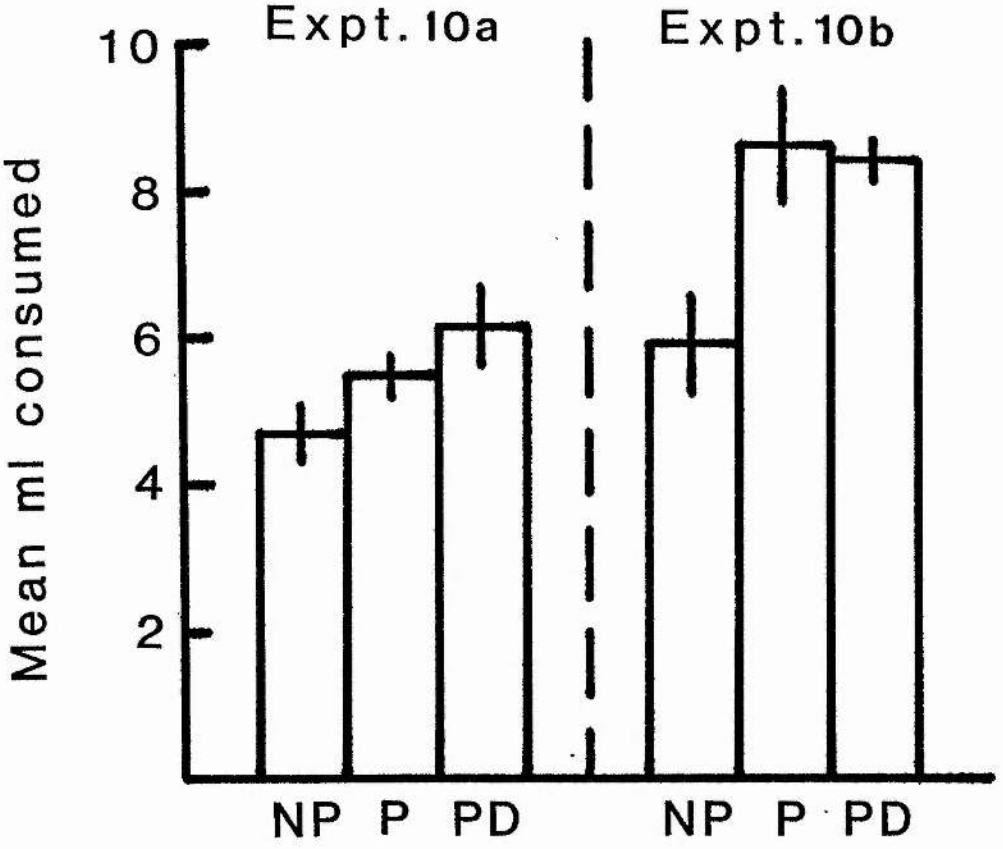

FIGURE 11. Mean consumption (ml) of 1.25% coffee solution by groups P, PD and NP during a 10-min test period in Experiments 10a and 10b.

ml and 2.31 ml). A 3 x 2 ANOVA performed on the data from Expt. 10b indicated that there was a significant effect of Group ($F(2, 21) = 8.88$, $p < .002$) and of Test ($F(1, 21) = 61.38$, $p < .0001$). There was, however, no Group x Test interaction ($F(2, 21) = 2.06$, $p > .10$). The Group data were therefore collapsed across Tests and subsequent a posteriori comparisons using the DMRT indicated that Group P and Group PD did not differ from one another in amount of lemon consumed, but both these groups drank significantly more lemon than did Group NP ($p < .01$).

The data from the 10-min coffee test in Expt. 10b are shown on the right of Figure 11. Group P and Group PD both drank more coffee (8.59 ml and 8.38 ml, respectively) than did Group NP (5.94 ml). A oneway ANOVA confirmed these differences in coffee consumption were reliable ($F(2, 21) = 5.14$, $p < .02$). A posteriori comparisons with the DMRT indicated that Group P and Group PD, while not differing from one another in the amount of coffee consumed, both drank significantly more of the coffee solution than did Group NP ($p < .01$). There was no evidence in Expt. 10b, therefore, that an aversion was conditioned to coffee in Group PD.

Discussion

On the basis of results from preceding experiments that employed a neophobia design, it was predicted that the coffee distractor would disrupt latent inhibition of conditioned taste aversion (CTA) to a preexposed sucrose solution while enhancing latent inhibition of CTA to a preexposed lemon solution. In the event, neither of these predictions received empirical support. In both Expt. 10a and 10b, rats given a distractor immediately after preexposure to the target solution (i.e., Group PD) did not differ from rats preexposed to the target solution only (i.e., Group P) in the strength of aversion exhibited to the target solution following its subsequent pairing with LiCl-induced toxicosis. In other words, the distractor was ineffective in either disrupting or enhancing latent inhibition of a CTA.

Given the procedural similarity of the preexposure phase of latent inhibition studies to that employed during the study of habituation; and given the similar response of latent inhibition and habituation to identical parameter manipulations, which prompted the assumption of a common process underlying both phenomenon that is best explained in terms of the Wagner (1976) model, the failure to obtain a distractor effect in Expts. 10a and 10b analogous to that obtained with an habituation procedure is surprising and

raises the question of whether the Wagner model does provide the best explanation of the process underlying latent inhibition.

The major alternatives to the Wagner explanation of latent inhibition are the theories proposed by Mackintosh (1975), by Lubow, Weiner and Schnur (1981), and by Pearce and Hall (1980). These theories, like that of Wagner, assume that non-reinforced presentation of a stimulus results in a decrement of a stimulus-specific learning rate parameter, α, thereby reducing the ability of that stimulus to subsequently enter into association with a US. What differentiates the 4 theories is the mechanism by which they propose changes in the value of α occur. Wagner assumes that a decrement in α to a preexposed stimulus arises because the occurrence of that stimulus on a conditioning trial is predicted by contextual cues; Mackintosh assumes that α diminishes because the preexposed stimulus does not itself uniquely predict the occurrence of any other event; the conditioned attention theory (CAT) of Lubow et al assumes that a decline in the value of α occurs because the absence of any effective event following preexposure to a stimulus acts as a US to condition inattention to that stimulus. Lastly, Pearce and Hall assume that α declines because the preexposed stimulus accurately predicts the non-occurrence of the US. According to the Pearce and Hall model, changes in the value of α are determined by the expression $(L - V)$, where L = the intensity of the US, and V

= the associative strength of the CS on Trial n - 1. The associability of a CS, i.e., , = 0 when it perfectly predicts its consequences, i.e., when (L - V) = 0. Thus, "When a novel stimulus is presented in the absence of a reinforcer, L will be 0, and, since the associative strength of the stimulus is also 0, the associability of the stimulus will decline."

Like the Wagner theory, the Mackintosh, the Lubow et al, and the Pearce and Hall theory all expect a disruption of latent inhibition if preexposure to a target stimulus is followed immediately by presentation of a distractor: Mackintosh, because the preexposed target stimulus is a better predictor of the onset of the distractor than any accompanying contextual cues and hence it suffers less decline in than does a similar preexposed stimulus not followed by a distractor; Lubow et al, because presentation of a distractor in close temporal proximity to a preexposed target stimulus disrupts conditioning of inattention to that stimulus; Pearce and Hall, because L for a distractor, unlike that for non-reinforcement, will have a non-zero value. Consequently, (L - V) will have some non-zero value in the former case. The associability of a preexposed target stimulus should thus decline less rapidly when followed by a distractor than when followed by non-reinforcement. The results of Expts. 10a and 10b are thus equally at variance with expectations derived from the Mackintosh (1975), the Lubow et al (1981), and the Pearce

and Hall (1980) theory.

While the 4 theories of latent inhibition discussed thus far are equally unable to account for the results of Expts. 10a and 10b, the Wagner model appears to provide a better explanation of latent inhibition in general than do the rival theories. Unlike the Wagner model, which proposes that the decrement in processing a preexposed CS paired with a US, when preexposure and conditioning trial are separated by a comparatively long ISI, is because the occurrence of the CS on the conditioning trial is predicted by other cues in the environment (i.e., retrieval-generated priming), Mackintosh proposes that a preexposed CS loses salience because the CS itself does not predict any event that is not already predicted by other cues in the environment. Thus the Wagner model, but not that of Mackintosh, predicts latent inhibition to be context-specific. Studies that employed a comparatively long ISI separating CS preexposure from the conditioning trial and changed the context between preexposure to a CS and the CS-US trial have reported a disruption of latent inhibition with an interoceptive CS paired with an interoceptive US (Rudy et al, 1977; Westbrook et al, 1981) and with an exteroceptive CS paired with an interoceptive US (Channell & Hall, 1983).

These studies are consistent also with CAT which postulates that a contextual change between CS preexposure and conditioning trial acts as an external inhibitor (c.f., Pavlov, 1927) restoring the attentional response to the preexposed CS and thereby increasing its associability with a US. CAT, unlike the Wagner model which can appeal to self-generated priming, is unable, however, to handle data demonstrating that latent inhibition with a relatively short ISI separating a preexposed flavour CS from a flavour-LiCl pairing is not affected by a change of context between preexposure and conditioning presentations of the flavour CS (Westbrook et al, 1981).

The Pearce and Hall model can account for the context specificity of latent inhibition when a long interval separates preexposure and conditioning presentations of the CS if one assumes that contextual cues and the preexposed CS are treated as a configural stimulus. Subsequent presentation of the CS in a new context would then be equivalent to a new configural stimulus, with correspondingly high associability. The assumption that contextual cues and the preexposed CS are treated as a configural stimulus calls for the Pearce and Hall model, however, to predict that latent inhibition should also be context-specific when preexposure and conditioning presentations of a CS are separated by only a short temporal interval. Unlike the Wagner model which can appeal to the

notion of self-generated priming, the Pearce and Hall model is therefore embarrassed by evidence that the proximal latent inhibition effect may be independent of context (Westbrook et al, 1981).

Although, therefore, alternatives to the Wagner interpretation of latent inhibition exist, the Wagner model is able to account for more of the data than are its competitors. That being so, the failure to obtain distractor effects in Expts. 10a and 10b in line with those predicted by the Wagner model must be addressed.

Several studies have examined the relationship between amount of flavour CS consumed on a conditioning trial and the strength of the resultant conditioned aversion. Smith and Morris (1963) found that the strength of aversion established to saccharin was uniform across CS amounts ranging from 4.6 ml to 9.2 ml. Similar results were reported by Barker (1976) who presented rats with saccharin ranging in amount from 0.0 ml to 10.0 ml and found that the strength of conditioned aversion reached asymptote with a CS exposure of 3.0 ml. Bond and DiGuisto (1975) presented rats with either 0.5, 1.5 or 5.5 ml saccharin and reported a monotonic increase in strength of aversion as CS exposure increased; the aversion to each CS amount tested being significantly different from that of the others. The Bond and DiGuisto study, however, employed multiple comparisons without attempting to control for inflation of the Type 1

error rate.

Braveman and Crane (1977) were only partially able to replicate the Bond and DiGuisto results. Braveman and Crane presented rats with either 0.5, 1.5, 5.5, 6.5 or 10.5 ml saccharin and obtained a U-shaped function: the aversion being weakest with a 0.5 ml and a 10.5 ml CS. The aversions to the two extreme values of CS amount tested were significantly different from all others: the latter did not differ from one another. Lastly, Deutsch (1978) found no difference in strength of aversion to a 1.0 ml or a 10.0 ml presentation of .15% saccharin solution that was paired 30-min later with LiCl.

These studies indicate that, within certain boundary limits (perhaps because of a floor effect), differences in the amount of CS paired with a toxicosis US are not readily translated into significant differences in the strength of conditioned aversion to the CS. It is possible, therefore, that processing of the target solution on the conditioning trial in Expts. 10a and 10b did vary in the manner predicted by the Wagner model, but not sufficiently to be reflected in any difference in strength of aversion to the target solution.

3.4.2 Experiments 11a and 11b

The absence of any evidence from Expts. 10a and 10b that a distractor may disrupt latent inhibition of taste aversion learning to a preexposed target solution is particularly surprising in view of the Best *et al* (1979) demonstration of such an effect with the use of procedures similar to those that were employed in Expts. 10a and 10b. Close examination of the reported procedure in the Best *et al* study, however, identifies a variable that may account for the discrepancy between their results and those of Expts. 10a and 10b. Although the target flavour (cider vinegar) and the distractor (vanilla) in the Best *et al* study were each nominally of 3% concentration, according to the Procedure section of the report, these concentrations were derived by mixing 3 parts cider vinegar (or 3 parts vanilla extract) with 7 parts tap water, but 3/(3+7) x 100 = 30% and not 3%. The Best *et al* results may be a function, therefore, of the strong flavour concentrations they apparently employed in their study. These fluid concentrations are 10 x greater than those normally used in flavour neophobia or CTA studies. Experiments 11a and 11b, therefore, sought to determine whether the disruption of LI by a distractor reported by Best *et al* is unique to the particular concentrations they used.

Expt. 11a used 30% cider vinegar as the target solution and 30% vanilla as the distractor to determine, first, whether the disruption of LI reported by Best et al (1979) could be replicated. Expt. 11b sought to determine whether the same effect could be obtained using 3% cider vinegar as the target solution and 3% vanilla as the distractor.

Method

Subjects

Forty-eight experimentally-naive female Lister rats, bred and reared in the Dept. of Psychology, University of St. Andrews, were housed and maintained in the same way as were rats in the preceding experiments. Twenty-four rats (150-198 g) were run in Expt. 11a; and 24 rats (158-198 g) in Expt. 11b.

Procedure

In all unspecified details, the procedure in Expts. 11a and 11b was identical to that of Expt. 10a. Three groups, i.e., Group NP, Group P and Group PD (each of n = 8) were run in each experiment. Throughout the experiments, rats were maintained on a 23.5 h fluid deprivation schedule. The target solution in Expt. 11a was 30% (v/v) cider vinegar; in Expt. 11b, the target solution was 3% (v/v) cider

vinegar. The distractor in Expt. 11a was 30% (v/v) vanilla solution; in Expt. 11b, the distractor was 3% (v/v) vanilla solution. In all other unspecified details, the procedure of Expts. 11a and 11b was identical.

On Day 1, the conditioning day, rats in Group P and Group PD were given a 5-min access to 7 ml cider vinegar. This was followed immediately by either a 5-min access to 7 ml of vanilla solution (Group PD), or water equivalent to the mean amount of vanilla consumed by Group PD (Group P). Rats in Group NP were allowed to drink water equivalent to the mean amount of vinegar and vanilla consumed during preexposure by Group PD. Four hours later, all rats in each group were allowed 5-min access to 7 ml cider vinegar. Thirty minutes later, all rats were given a 10 ml/kg i.p. injection of .15M LiCl.

On Day 2, all rats were given a 10-min presentation of water in the test box, followed by 20-min access to water in the home cage. On Day 3 and on Day 4, all rats were given a 10-min presentation of the vinegar solution in the test box, while on Day 5 all rats were given a 10-min presentation of the vanilla solution. Following the test sessions on Days 3-5, all rats were allowed 20-min access to water in the home cage.

Results

The data for vinegar consumption in each experiment are shown in Figure 12 (Expt. 11a) and in Figure 14 (Expt. 11b). The amount of vinegar consumed by each group during the 5-min period of access that preceded the LiCl injection by 30-min is shown on the left of Figs. 12 and 14; the amount of vinegar consumed by each group during the two 10-min post-conditioning tests of aversion to vinegar are shown on the right of Figs. 12 and 14. The data from the 10-min vanilla test are shown in Fig. 13 (Expt. 11a) and Fig. 15 (Expt. 11b).

In Expt. 11a, Group P drank more vinegar on the conditioning trial (i.e., 0.34 ml) than did Group NP (0.20 ml), while the vinegar intake of Group PD (0.23 ml) was intermediate between that of Group P and Group NP. These differences, however, were not statistically significant ($F(2, 21) = 1.30$).

The groups did not drink comparable amounts of vinegar on the post-conditioning tests. On Test 1, Group PD drank 0.24 ml, Group P drank 0.16 ml and Group NP drank 0.09 ml. On Test 2, Group PD drank 0.41 ml, Group P drank 0.19 ml and Group NP also drank 0.19 ml. A 2 x 3 ANOVA on the data from the two vinegar tests indicated that there was a reliable difference in consumption between Groups ($F(2, 21) = 4.91$,

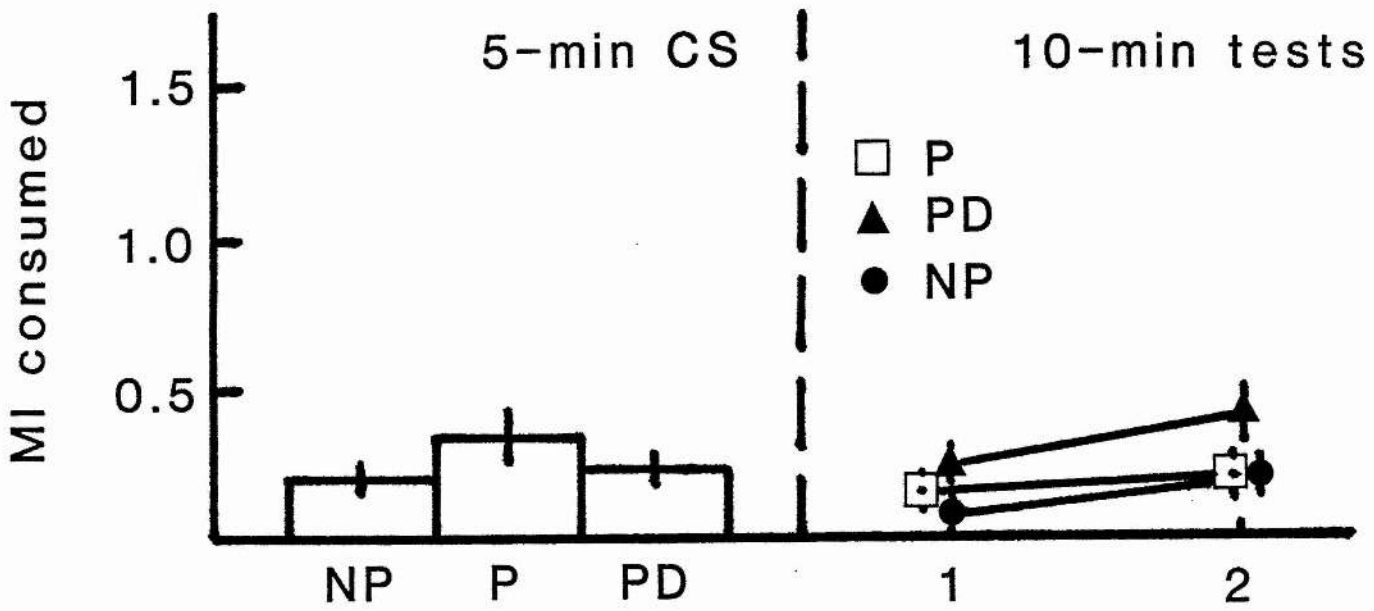

FIGURE 12. Mean consumption (ml) of 30% vinegar solution by groups P, PD and NP on the conditioning trial (left panel) and on the post-conditioning tests of latent inhibition (right panel) in Experiment 11a.

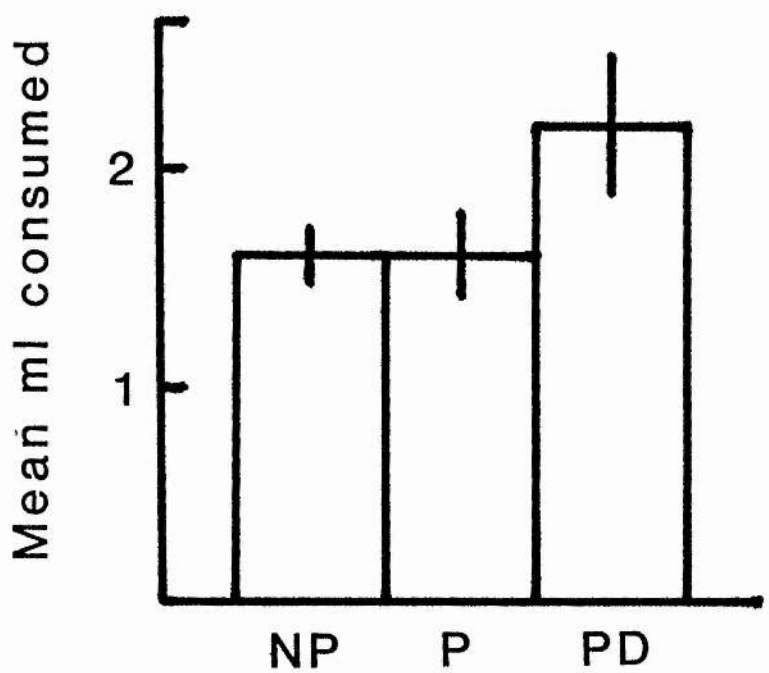

FIGURE 13. Mean consumption (ml) of 30% vanilla solution by groups P, PD and NP during a 10-min test period in Experiment 11a.

$p < .05$) and between Trials ($F (1, 21) = 6.77$, $p < .05$), but there was no Group x Trial interaction effect ($F (2, 21) = 0.94$). Accordingly, the vinegar consumption of each rat was pooled across trials. Comparisons made with the DMRT indicated that Group PD drank reliably more than did rats in Group NP or in Group P (both ps $< .05$). Group P did not differ from Group NP in the amount of vinegar consumed ($p > .10$). Thus, Group PD (but <u>not</u> Group P) evidenced a latent inhibition effect. There was no difference between the three groups in the amount they consumed (means = 1.56-2.19 ml) on the vanilla test ($F (2, 21) = 1.08$).

In Expt. 11b, as was the case in Expt. 11a, Group P drank more vinegar on the conditioning trial (i.e., 3.25 ml) than did Group NP (2.15 ml). Again, the vinegar intake of Group PD (2.45 ml) was intermediate between that of Group P and Group NP, but these differences were not statistically significant ($F (2, 21) = 1.97$, $p > .10$).

The groups did not drink comparable amounts of vinegar on the post-conditioning tests. On Test 1, Group PD drank 4.40 ml, Group P drank 4.35 ml and Group NP drank 1.45 ml. On Test 2, Group PD drank 4.83 ml, Group P drank 4.53 ml and Group NP drank 3.54 ml. A 2 x 3 ANOVA indicated that there was a reliable difference in vinegar consumption between Groups ($F (2, 21) = 11.20$, $p < .001$) and between Tests ($F (1, 21) = 12.93$, $p < .005$). There was also a significant Group x Test interaction ($F (2, 21) = 5.80$, $p < .05$). The

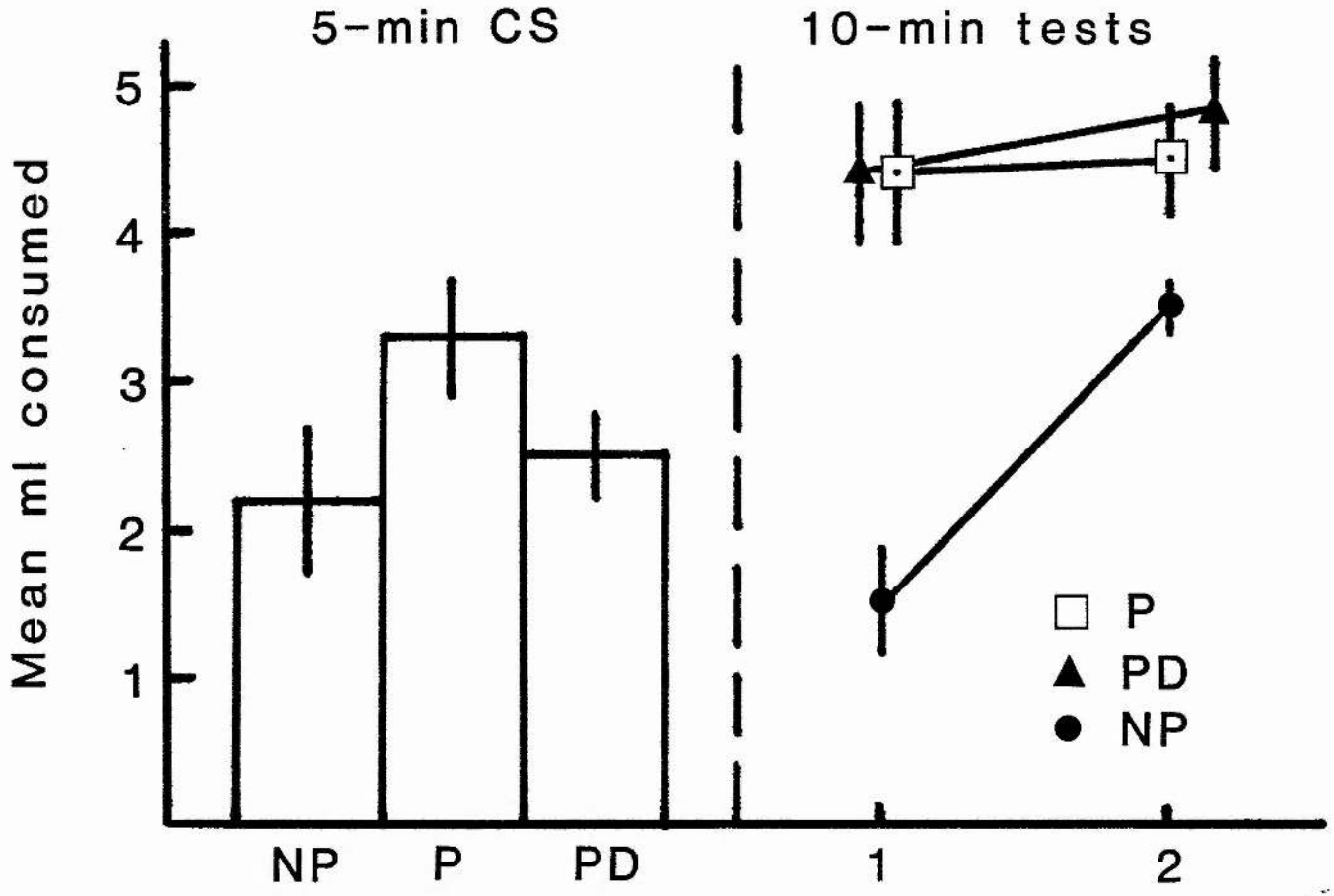

FIGURE 14. Mean consumption (ml) of 3% vinegar solution by groups P, PD and NP on the conditioning trial (left panel) and on the post-conditioning tests of latent inhibition (right panel) in Experiment 11b.

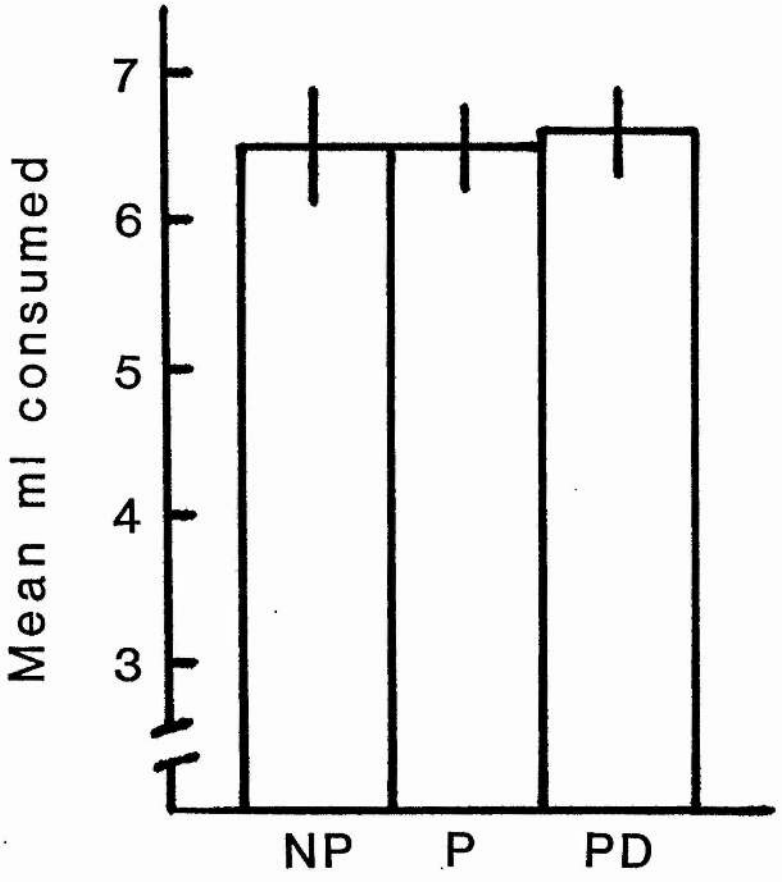

FIGURE 15. Mean consumption (ml) of 3% vanilla solution by groups P, PD and NP during a 10-min test period in Experiment 11b.

latter was attributable to the performance of Group NP. Whereas neither Group PD ($t(7) = 2.08$, $p > .05$) nor Group P ($t(7) = .76$) reliably increased their fluid intake from Test 1 to Test 2, Group NP drank significantly more vinegar on Test 2 than on Test 1 ($t(7) = 8.60$, $p < .0001$). A posteriori comparisons with the DMRT indicated that Group PD and Group P drank comparable amounts of vinegar on Test 1 and Test 2 (both ps $> .10$). On Test 1, Group PD and Group P both drank significantly more vinegar than did Group NP ($p < .01$). On Test 2, Group PD continued to drink reliably more vinegar solution than did Group NP ($p < .05$), but the amount consumed by Group P did not reliably differ from the amount consumed by Group NP ($p > .10$). There was no difference between the three groups in the amount of vanilla consumed (means 6.49-6.59) on the 10-min test ($F(2, 21) = .02$).

Discussion

Neither in Expt. 11a, nor in Expt. 11b, was there any evidence that latent inhibition of a CTA is disrupted by a flavour distractor. This null effect is consistent with the results of Expts. 10a and 10b and with those reported by Westbrook *et al* (1982), but is inconsistent with those reported by Best *et al* (1979).

Westbrook et al speculated that the discrepancy between the results of their study and those obtained by Best et al might be due to differences in duration of CS exposure in the two studies, i.e., 2-min (Westbrook et al) versus 5-min (Best et al). In the light of the results of Expts. 11a and 11b, however, in which CS exposure duration was 5-min, this variable does not appear sufficient to account for these discrepant findings. Expts. 11a and 11b did not, of course, fully replicate the conditions and procedures of the Best et al study. Further work will be necessary, therefore, to determine which of the remaining procedural differences is (or are) responsible for the disruption of latent inhibition effect obtained by Best et al.

3.4.3 Experiment 11c

Expt. 11c employed a distractor (30% vanilla) more powerful vis-a-vis the target solution (3% cider vinegar) than was the case in Expts. 11a and 11b in a further attempt to disrupt latent inhibition of a CTA.

Method

Subjects

Twenty-four experimentally-naive female rats (156-196 g), bred and reared in the Dept. of Psychology, University of St. Andrews, were housed and maintained in the same way as rats in the preceding experiments.

Procedure

In all unspecified details, the procedure in Expt. 11c was identical to that of Expt. 11a. There were three groups of rats, each of n = 8. On Day 1, the conditioning day, Group P and Group PD received a 5-min access to 7 ml of 3% (v/v) cider vinegar, followed immediately by a 5-min access to 7 ml of 30% (v/v) vanilla solution (Group PD) or water equivalent to the mean amount of vanilla consumed by Group PD (Group P). Group NP were allowed to drink water equivalent to the mean amount of vinegar and vanilla consumed by Group PD during preexposure. Four hours later, all rats were allowed 5-min access to 7 ml of cider vinegar. This was followed 30-min later by a 10 ml/kg i.p. injection of .15M LiCl.

Following a recovery day, all rats were given a 10-min test presentation of vinegar on Day 3 and a 10-min test presentation of vanilla on Day 4.

Results

The amount of vinegar consumed by the three groups on the conditioning trial is shown on the left of Figure 16; the amount of vinegar consumed by the three groups on the 10-min post-conditioning test is shown on the right of Fig. 16. The data from the 10-min vanilla test are shown in Figure 17.

The groups drank different amounts of vinegar on the conditioning trial ($F(2, 21) = 21.0$, $p < .0001$). Group NP drank 3.70 ml, Group PD drank 4.85 ml, and Group P drank 6.28 ml. Multiple comparisons with the DMRT indicated that Group P drank more vinegar than did either Group PD or Group NP ($p < .01$) and that Group PD drank more vinegar than did Group NP ($p < .01$). The groups also drank different amounts of vinegar solution on the 10-min post-conditioning test ($F(2, 21) = 14.37$, $p < .001$). Whereas Group P and Group PD drank an identical amount (i.e., 5.46 ml), this was significantly greater than the amount (2.62 ml) consumed by Group NP (DMRT: $p < .01$). There was no difference, however, in the fluid intake of the three groups (means = 2.03-2.58 ml) during the 10-min vanilla test ($F(2, 21) = .20$).

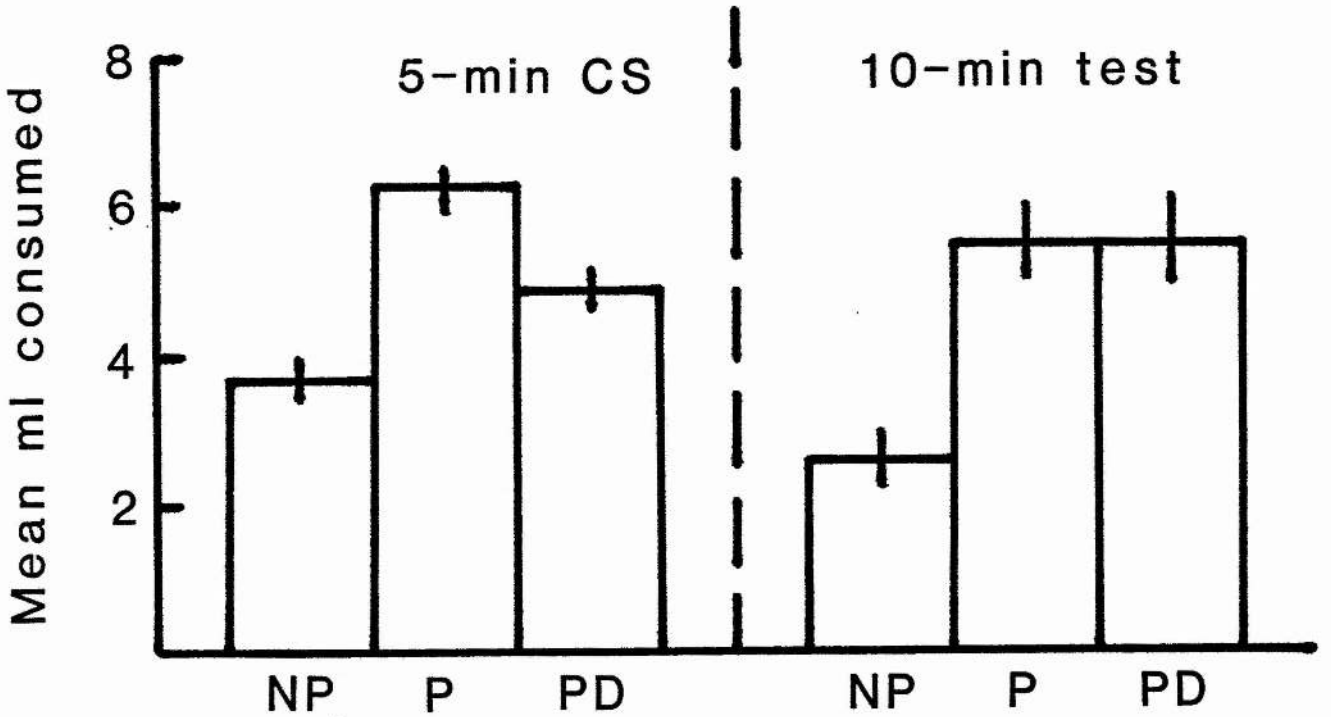

FIGURE 16. Mean consumption (ml) of 3% vinegar solution by groups P, PD and NP on the conditioning trial (left panel) and on the post-conditioning test of latent inhibition (right panel) in Experiment 11c.

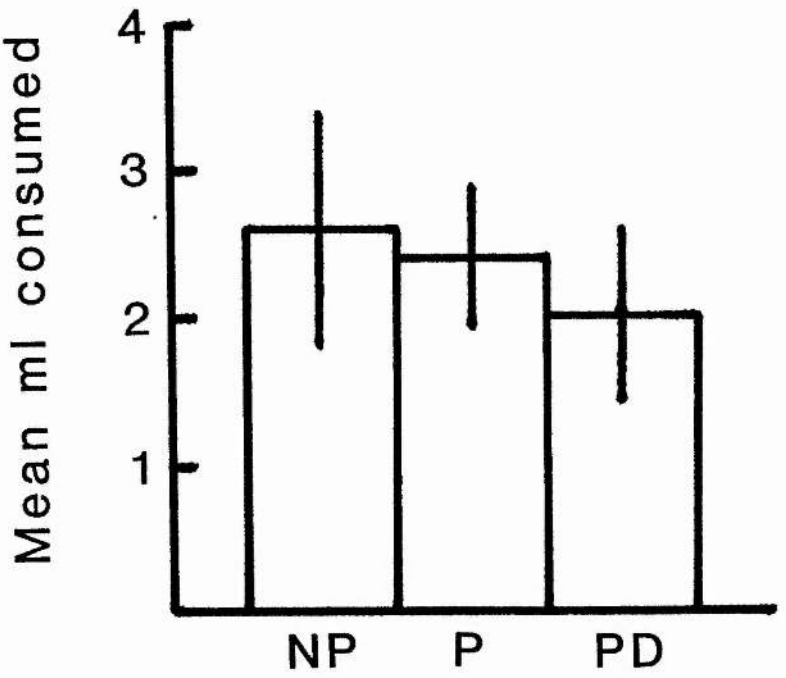

FIGURE 17. Mean consumption (ml) of 30% vanilla solution by groups P, PD and NP during a 10-min test period in Experiment 11c.

Discussion

In Expts. 10a and 10b, the amount of target solution rats drank during the CS-US pairing was controlled in order to ensure that there was no difference between groups in the amount of target solution paired with LiCl. In Expts. 11a, 11b and 11c, subject to the limitation that intake could not exceed 7.0 ml, no attempt was made to ensure that groups consumed equivalent amounts of target solution on the conditioning trial. The amount of target flavour consumed on the conditioning trial in Expts. 11a, 11b and 11c (but not in Expts. 10a and 10b) provides, therefore, an index of the strength of neophobia elicited by the target solution as a function of preexposure treatment.

In both Expt. 11a and 11b, preexposure to the target solution somewhat attenuated neophobia to that solution, as is indicated by the greater amount of vinegar consumed by Group P on the conditioning trial compared to the amount consumed by Group NP. More interestingly, rats that experienced a distractor following preexposure to the vinegar solution exhibited a degree of neophobia towards the vinegar on the conditioning trial that was intermediate between that shown by Groups P and NP. This pattern of results was replicated in Expt. 11c and shown to be a reliable effect. In Expt. 11c, Group PD drank significantly less vinegar solution on the conditioning

trial than did Group P, although both groups had the same amount of previous experience with the vinegar solution. (It should be noted that this effect is understated because of the limitation imposed on the amount that rats were allowed to drink on the conditioning trial, i.e., four of the eight rats in Group P were removed from the test box before 5 minutes elapsed in order to prevent them drinking more than 7.0 ml, whereas no rats in Group PD were so removed).

The demonstration in Expt. 11c that a distractor may disrupt habituation of neophobia to a preexposed target solution without affecting the strength of latent inhibition to that solution provides direct evidence in support of the suggestion made when discussing the results of Expts. 10a and 10b, i.e., that the memorial processing of the target flavour on the conditioning trial may have varied as a function of preexposure experience in the manner predicted by the Wagner model, but not sufficiently to be reflected in differences in strength of aversion conditioned to the target flavour.

A methodological point to note is that the strength of aversion exhibited by Groups P and PD towards the target solution during testing in Expt. 11c could potentially have been affected by the different amounts of vinegar consumed by the two groups on the conditioning trial, thereby making it difficult to conclude whether the response to vinegar

during testing reflected the degree of latent inhibition to vinegar resulting from the preconditioning experience or simply the amount of vinegar paired with LiCl.

While there is evidence to show that the amount of solution drunk on the conditioning trial can affect the strength of aversion subsequently exhibited towards the flavour CS, this evidence relates to the use of saccharin as the CS. No comparable series of studies have explored the relationship between the amount of vinegar solution paired with toxicosis and the strength of the subsequently exhibited aversion to vinegar. This may or may not be similar to the function relating these two variables, i.e., amount of CS and magnitude of CR, when saccharin is the CS. It is difficult, therefore, to say whether, on the basis of the amount of vinegar paired with LiCl on the conditioning trial, one might have expected Group PD to show an aversion to vinegar that was less than, more than, or equivalent to, that shown by Group P during testing in Expt. 11c.

The available evidence with regard to saccharin is that the conditioned aversion reaches asymptote when the CS amount is equal to 3.0 ml (Barker, 1976) and that the strength of the conditioned aversion is uniform across CS amounts ranging from 4.6-9.2 ml (Braveman & Crane, 1977; Smith & Morris, 1963). If this relationship is true also of vinegar paired with toxicosis, this would suggest that the different amounts consumed by Group P and Group PD on the

conditioning trial in Expt. 11c (i.e., 6.3 and 4.9 ml, respectively) ought, of itself, to have had little or no influence on the strength of aversion conditioned to vinegar in the two groups. In other words, responding to vinegar during testing ought to have represented the strength of latent inhibition to vinegar uncontaminated by any difference in conditioned strength attributable to the amount of CS paired with LiCl.

4 OVERSHADOWING AND POTENTIATION OF CTA

When a compound CS is paired with a US, the elements comprising the compound CS do not acquire equal associative strength (Pavlov, 1927). If one of the elements is more salient than the other, because of its greater intensity (Kamin, 1969) or because of its greater validity in predicting the occurrence of the US (Wagner, Logan, Haberlandt, & Price, 1968) or because of its closer temporal contiguity to the US (Mackintosh & Reese, 1979), or because, although both elements are equally temporally contiguous with the US, i.e., offset of both CS elements coincides with the onset of the US, the onset of one element precedes the onset of the other element (Egger & Miller, 1962), that element will capture most of the associative strength accrueing from the pairing of the compound CS with the US. Consequently, the less salient element of the compound will elicit a weaker CR than it would had the same element been paired separately with the US. This phenomenon has been called overshadowing.

4.1 Theoretical explanations of overshadowing

Theoretical explanations of overshadowing have been proposed by Mackintosh (1975) and by Rescorla and Wagner (1972). Both accounts assume that the more salient element of a compound CS conditions (i.e., acquires associative strength) faster than does the less salient element, thereby

becoming the more reliable predictor of the occurrence of the US. However, whereas Mackintosh assumes that animals learn to ignore the less reliable predictor of the US, Rescorla and Wagner assume that, as the US becomes increasingly well-predicted by the more salient CS element, it (the US) becomes less able to reinforce conditioning to the less salient CS element.

4.1.1 Rescorla and Wagner (1972)

According to Rescorla and Wagner, on any given trial, the increase in associative strength to a CS, ΔA, on that trial, when that stimulus is paired separately with a US, can be represented by the following expression:

$$\alpha a B(L - Va)$$

where L = the maximum associative strength of which the US is capable of supporting

Va = the net associative strength of stimulus A on the preceding trial, i.e., Trial n-1

αa = a learning-rate parameter specific to CSA which reflects the 'salience' of CSA

and B = a learning-rate parameter for that particular US

When a compound CS, AX, is paired with a US, the associative strength of each element of the CS must be taken into account when computing the ability of the US, on any particular trial, to increase the associative strength of the elements comprising the compound CS. Thus, on any given

trial, the associative strength of CSA increases in accordance with the following expression:

$$\propto aB((L - (Va + Vx)).$$

On the first conditioning trial, neither A nor X have any associative strength, i.e., Va and Vx both equal zero, hence, regardless of whether A is paired separately with a US or is conditioned in compound with X, the increase in associative strength to A on Trial 1 will be equal to $\propto aB(L)$. In other words, the Rescorla and Wagner model predicts no overshadowing of A by X on the first conditioning trial. As a consequence of both A and X acquiring some associative strength on Trial 1, however, ((L - (Va + Vx)) will be less than (L - Va) on trial 2 and the increase in associative strength to A will therefore be less when it is conditioned in compound with X than when it is paired separately with the US, i.e., overshadowing of A by X may be observed on Trial 2.

4.1.2 Mackintosh (1975)

Unlike Rescorla and Wagner, Mackintosh assumes that the stimulus-specific learning-rate parameter $\propto$ may change during the course of conditioning to reflect the relative reliability with which that CS predicts the occurrence of the US. On the first conditioning trial, neither element of a compound CS, AX, predicts the occurrence of the US any better than the other, consequently, A will acquire the same

amount of associative strength whether it is conditioned separately or in compound with X. However, if αX is initially greater than αA, i.e., if X is more salient than A, then X will acquire more associative strength on Trial 1 than does A, with the result that α for A in the compound CS condition will decline relative to α for A in the single CS condition. On Trial 2, therefore, A will acquire less associative strength when it is conditioned in compound with X than it does when paired separately with the US.

From the above description of the Rescorla and Wagner (1972) and the Mackintosh (1975) explanations of overshadowing, it is evident that neither theory allows overshadowing to occur on the first conditioning trial. A more recent theory proposed by Pearce and Hall (1980) also fails to predict the occurrence of overshadowing on a single trial.

4.1.3 Pearce and Hall (1980)

The Pearce and Hall theory differs from that of Rescorla and Wagner in that it assumes that the reinforcing property of the US remains constant over trials, i.e., the maximum associative strength of which the US is capable of supporting is equal to L on each trial (c.f., Rescorla & Wagner (1972), in which the reinforcing capacity of the US on each trial is determined by (L-Vax)), and that the course of conditioning to a CS is determined by changes in α to

that CS. The Pearce and Hall theory differs from that of Mackintosh, however, in that Pearce and Hall assume that α for a particular CS decreases from an initial value close to L until it, the CS, becomes a reliable predictor of the occurrence of the US, at which point no further increase in associative strength accrues to that CS.

Pearce and Hall argue that the associative strength of a CS (not to be confused with the associability of a CS, i.e., α) increases until it equals the maximum supportable (i.e., L) by the US. They further assume that the elements of a compound CS will each increase in associative strength until their <u>combined</u> associative strength is equivalent to L. Neither element of a compound CS will therefore acquire as much associative strength as would the same element if paired separately with the US, i.e, reciprocal overshadowing would be predicted. However, since, ordinarily, neither element of a compound CS will have any associative strength prior to Trial 1, the increment in associative strength to a CS on the first conditioning trial should be the same regardless of whether that CS is conditioned separately or in compound with another CS, i.e., overshadowing is not predicted on Trial 1.

Despite the uniformity with which the theories so far discussed deny the possibility of obtaining overshadowing on the first conditioning trial, one-trial overshadowing has been reported (James & Wagner, 1980; Mackintosh, 1971;

Mackintosh & Reese, 1979; Revusky, 1971). The theories proposed by Mackintosh (1975), Pearce and Hall (1980), and Rescorla and Wagner (1972) do not, therefore, appear to provide an adequate account of all the data on overshadowing.

4.1.4 Wagner (1976)

Wagner's (1976) model predicts overshadowing to occur because the elements of a compound CS compete for access to the limited processing capacity of STM. Neither element of the CS compound will therefore command as much processing in STM as would be the case if each element was presented separately. Since the strength of the association formed between events is asumed to be a direct function of the extent of temporal overlap in the processing of these events in STM, and the length of time a stimulus occupies STM is assumed to be directly related to the amount of processing it elicits, elements of a compound CS are therefore likely to form a weaker associaton with a US than would be the case if each element was paired separately with the US. The Wagner model, therefore, predicts that overshadowing may be observed after a single trial and that such overshadowing may be reciprocal, i.e., each element of a compound CS may acquire less associative strength than would have been the case if that element had been conditioned separately. Evidence supporting the existence of one-trial overshadowing has already been presented. With regard to the second

prediction of the Wagner model, recent evidence has been obtained of reciprocal overshadowing (Bond, 1983; Bouton & Whiting, 1982).

4.2 Overshadowing of CTA

Apparent demonstration of overshadowing in a taste aversion paradigm has been reported by Lindsey and Best (1975), and by Revusky (1971). Lindsey and Best (1975) paired an olfactory cue (0.08% vanilla) with a flavour (0.15% saccharin). The vanilla and the saccharin were presented sequentially with a zero second (i.e., no) delay and with order of presentation counterbalanced. After experiencing both CS elements, the rats were injected immediately with apomorphine. Control animals received the same presentation of CS elements but were injected with saline. On a subsequent two-bottle test, in which rats were given the opportunity to drink either saccharin or a familiar orange solution, the experimental animals exhibited a significantly weaker preference for the saccharin than that exhibited by the controls. When offered the choice of drinking vanilla or familiar orange, however, experimental and control rats did not differ in their preference for the vanilla, i.e., the saccharin completely overshadowed the vanilla in the experimental group.

Unfortunately, Lindsey and Best did not run a control group of rats injected with apomorphine after consuming vanilla only. In the absence of evidence that apomorphine-induced toxicosis will condition an aversion to an 0.08% vanilla solution presented separately, the failure of the experimental group in the Lindsey and Best study to exhibit a reduced preference for the vanilla relative to the preference exhibited by the saline-injected controls need not be attributed to overshadowing by the saccharin.

The failure of Lindsey and Best to include a control group made ill after consuming the vanilla alone is a serious omission in view of evidence that aversions are not readily conditioned to vanilla. Although LiCl may condition an aversion to many solutions with a CS-US interval in the order of 4-6 hours, Best et al (1979) were unable to condition an aversion to a 30% vanilla solution with a 90-min CS-US interval. Similarly, Kalat and Rozin (1970) were unable to condition an aversion to a .17% vanilla solution with a 15-min CS-US interval.

The most relevant study to compare with that of Best and Lindsey (1975), since it involved injecting rats with apomorphine immediately after they had consumed a 0.08% vanilla solution, is that of Best (1975). The Best study was designed to determine whether conditioned inhibition could be demonstrated in a conditioned taste aversion

paradigm. Three groups of rats were run (Best, 1975; Expt. 1). One group received saccharin paired with injection of apomorphine (Cond Inhib); one group received saccharin only (No-ill Control); and one group received saccharin and injection of apomorphine separately presented (Ill Control). All 3 groups subsequently received a 2-min presentation of saccharin followed immediately by a 10-min presentation of saline, with no aversive consequences. This procedure was designed to establish saline as a conditioned inhibitor in Group Cond Inhib. To provide an excitatory context within which to assess the effectiveness of saline as a conditioned inhibitor, Best injected all 3 groups with apomorphine immediately after they had consumed 0.08% vanilla solution. All 3 groups were later offered the choice of drinking either vanilla or saline on a two-bottle preference test. The experimental prediction was that Group Cond Inhib would show a greater preference for the saline than did either of the two control groups, and this was confirmed.

Leaving aside the question of how secure the Best result is, given the wide overlap that existed in the ranges of all 3 groups and the fact that the claim for a significant difference between the experimental rats and controls depended upon the use of multiple non-parametric comparisons with no attempt to control for the inflation of the Type 1 error rate that results from this procedure, of more immediate concern is that neither in this experiment,

nor in a subsequent replication (Best, 1975; Expt. 2), did Best include a group injected with saline after consuming the vanilla solution and then tested with vanilla alone. This would have permitted a conclusion as to whether or not apomorphine did condition an aversion to vanilla. A comparison of the relative preference for saline over vanilla exhibited by the two control groups in Expt.1 of the Best study strongly suggests that it did not. Neither of these controls showed a preference for saline over vanilla; this, despite the fact that the comparison was between a saline solution that the rats had previously experienced and knew to have no aversive consequences and a vanilla solution to which a conditioned aversion had supposedly been established! There is no empirical evidence, therefore, that drug-induced toxicosis will condition an aversion to a 0.08% vanilla solution with a 0-2.5 minute CS-US interval and hence no compelling reason to interpret the Lindsey and Best (1975) results as evidence of overshadowing.

Until recently (see Bond, 1983; Bouton & Whiting, 1982; Mikulka, Pitt, & Philpott, 1982), the burden of proof for the existence of overshadowing in a CTA paradigm rested upon the Revusky (1971) study. Revusky injected several groups of rats with LiCl 75-min after they had been allowed to drink 2 ml of 0.2% saccharin solution. Experimental rats who were given 5 ml of 0.5, 1.5 or 4.5% vinegar solution 15-min after presentation of the saccharin (and hence 60-min prior to the LiCl-US) exhibited a weaker aversion to the

saccharin than did rats that were not presented with vinegar during the saccharin-LiCl interval. No controls were run, however, to permit a conclusion as to whether the vinegar distractor overshadowed the saccharin because it was more salient than the saccharin or because it occurred in closer temporal contiguity to the LiCl than did the saccharin.

4.3 Potentiation of CTA

Recent taste aversion studies have found results opposite to that of overshadowing, viz., a stimulus elicited more avoidance during testing if it had previously formed part of a compound CS paired with LiCl than if it had been paired separately with LiCl. Potentiation, rather than overshadowing, has been found when a visual cue is paired with a flavour and followed by toxicosis in both pigeons and quail (Clarke, Westbrook, & Irwen, 1979; Lett, 1980), and in rats (Galef & Osborne, 1978) and when an olfactory cue is paired with a flavour and followed by toxicosis in rats (Durlach & Rescorla, 1980; Rusiniak, Hankins, Garcia, & Brett, 1979; Westbrook, Homewood, Horn, & Clarke, 1983).

The initial demonstration that rats acquire a stronger aversion to an olfactory cue when it is conditioned in compound with a flavour solution than when it is conditioned separately (i.e., Rusiniak et al, 1979) depended on a comparison of different groups from separate experiments. Later better designed studies by Durlach and Rescorla (1980)

and Westbrook *et al* (1983) appeared to establish potentiation of an odour aversion on a sounder footing (but see Bond, 1983; Bouton & Whiting, 1982; Mikulka *et al*, 1982; for failures to replicate potentiation of a conditioned odour aversion).

4.4 Theoretical explanations of potentiation

Several theoretical explanations of potentiation share the common assumption that the more salient taste cue makes possible a stronger association between the less salient CS and the US, although they differ in the precise mode of action attributed to the taste CS. Galef and Osborne (1978) suggested that potentiation occurs because the taste cue brings to the organism's attention stimulus attributes of the less salient cue that would not otherwise have been heeded. As a result of this "directed attention" function of the taste cue, a more elaborate memorial representation of the less salient cue is made possible, thereby permitting the formation of a stronger association of that otherwise weak cue with the toxicosis US. An alternative possibility is that the taste cue acts to bridge the temporal interval separating presentation of the less salient cue and the occurrence of the US, thereby allowing the weak cue to form a stronger association with the US (Rescorla, 1982). Lastly, a taste cue may "protect" a less salient cue from habituation (c.f., Pfautz, Donegan, & Wagner, 1978) thereby allowing the latter to enter into a stronger association

with the US.

In contrast to the foregoing explanations of potentiation, Durlach and Rescorla (1980) have argued that potentiation is the result, not of a stronger association between the less salient CS and the US, but of an association formed between the elements of the compound CS. This latter association allows the less salient element to augment the associative strength resulting from its direct association with the US with some associative strength "borrowed" from its partner in the CS compound, thereby producing a potentiation effect.

In support of their hypothesis, Durlach and Rescorla (1980) demonstrated that if the extra source of associative strength available to an odour CS conditioned in compound with a more salient taste cue was removed by post-conditioning extinction of the aversion to the taste CS then the strength of aversion exhibited to the odour cue was reduced. This result, however, does not provide unequivocal support for the Durlach and Rescorla hypothesis.

Granted that an association is formed between the elements of a compound CS, potentiation may nevertheless not be the result of the less salient CS "borrowing" associative strength from the more salient CS. Instead, an association between the CS elements may prolong STM processing of the less salient CS, thereby allowing that CS to acquire greater

associative strength by increasing the likelihood of conjoint processing of the less salient CS and the US. The Durlach and Rescorla (1980) data are compatible with either of these hypotheses: Extinction of the conditioned aversion to the taste CS may have produced a corresponding decrease in the strength of the aversion exhibited to the odour CS by weakening the odour-US association, i.e., presentation of the taste CS may have evoked a representation of the odour CS in the absence of the illness US, thereby occasioning mediated extinction of the odour-US association (c.f., Holland & Forbes, 1983; Holland & Ross, 1981).

4.5 PRESENT STUDIES

4.5.1 Experiments 12a and 12b

In Experiments 10a and 10b, an attempt to use knowledge derived from the preceding habituation of neophobia experiments regarding the memorial processing accorded to pairs of sequentially presented novel fluids that differed in their degree of similarity one to another, to predict the outcome of a conditioning procedure (latent inhibition) was unsuccessful. In Experiments 12a and 12b, an attempt was made to use prior knowledge about the nature of the stimulus interaction that results from the sequential presentation of two novel fluids differing in their degree of similarity to one another to predict the outcome of a different

conditioning procedure, i.e., overshadowing/potentiation of a CTA.

Rescorla (1980) demonstrated that interstimulus associations were promoted more by simultaneous than by sequential presentation of the CS elements. Rescorla and Durlach (1981), accordingly, compared the effectiveness of these different modes of stimulus presentation on the strength of the aversion acquired by an odour (1.5% banana or 1.5% almond) conditioned in the presence of a more salient taste cue (0.6% saccharin). They found that the taste cue potentiated conditioning to the odour CS when odour and taste were presented simultaneously, but overshadowed conditioning to the odour CS when odour and taste cues were presented sequentially. Rescorla and Durlach interpreted this result as support for the Durlach and Rescorla (1980) hypothesis that potentiation depends on the existence of an association between the CS elements paired with the US.

The banana and almond solutions (odour: no taste) used by Rescorla and Durlach were dissimilar to the other CS element, saccharin (no odour: sweet taste). Given the demonstration by Rescorla and Furrow (1977) that interstimulus associations are formed more rapidly between similar stimuli than between dissimilar stimuli, Expts. 12a and 12b sought to examine the possibility that sequential presentation of CS elements may not invariably result in

overshadowing of a CTA. Specifically, it was anticipated that sequential presentation of similar stimuli (i.e., lemon and coffee) might result in poteniation of a conditioned aversion to the lemon solution, whereas sequential presentation of dissimilar stimuli (i.e., sucrose and coffee) might result in overshadowing of a conditioned aversion to the sucrose solution.

Two groups of rats were run in each experiment. One group received a sequential presentation of a target solution and a distractor followed by injection of LiCl. The strength of aversion to the target solution was later compared to that shown by a control group which received the target solution separately paired with LiCl. The distractor in both experiments was a coffee solution. The target solution in Expt. 12a was sucrose and in Expt. 12b it was lemon. The coffee was expected to overshadow an aversion to sucrose in Expt. 12a, but to potentiate an aversion to lemon in Expt. 12b.

Method

In all unspecified details, the procedure and apparatus were identical to those of Expt. 1.

Subjects

Twenty-three experimentally-naive female Lister rats, bred in the Psychology Dept., University of St. Andrews,

were housed and maintained in the same way as were rats in preceding experiments. Eleven rats (124-184 g) were run in Expt. 12a; and 12 rats (147-184 g) in Expt. 12b.

Procedure

Expts. 12a and 12b each contained two groups, viz., Group E (n = 6 in both Expt. 12a and 12b) and Group C (n = 5 in Expt. 12a; n = 6 in Expt. 12b). The target solution in Expt. 12a was 5% (w/v) sucrose; and in Expt. 12b, 3% (v/v) lemon. The distractor in both experiments was 1.25% (w/v) coffee solution. Rats in Expt 12a were given a single 10-min test of conditioning to sucrose; rats in Expt. 12b were given two 10-min tests of conditioning to lemon. In all other respects, the procedure in Expts. 12a and 12b was identical.

The rats were placed on a 23.5 hour per day water deprivation schedule and accustomed to drinking in the test box. On Day 1, the conditioning day, all rats were given a 5-min presentation of the target solution. This was followed by an immediate 5-min presentation of the distractor to rats in Group E, whereas rats in Group C received immediate presentation of an amount of water equivalent to the mean amount of distractor solution drunk by rats in Group E. Sixty minutes after presentation of the target solution, all rats were given a 10 ml/kg i.p. injection of .15M LiCl.

On Day 2 and Day 3, all rats were presented with the daily ration of water in the test box. On Day 4, the test day, all rats were presented with the target solution in the test box and the amount ingested during a 10-min period was recorded. Since the direction of the difference in amount of target solution ingested by Group E and Group C in both Expt. 12a and 12b was specified a priori, test data were analysed using a one-tailed test of probability.

Results

The data from the post-conditioning tests of aversion to the target solution are shown in Figure 18 (Expt. 12a) and in Figure 19 (Expt. 12b).

In Expt. 12a, the amount of sucrose consumed by Group E on the 10-min test (i.e., 8.70 ml) was greater than that (6.36 ml) which was consumed by Group C. This difference was reliable ($t(9) = 1.99$, $p < .05$). Rats that experienced a coffee solution during the interval separating the conditioning presentation of sucrose from the lithium chloride US thus acquired a weaker aversion to sucrose than did rats that experienced sucrose paired separately with LiCl, i.e., coffee appeared to overshadow conditioning of an aversion to sucrose in Group E. The opposite pattern of results, however, was obtained in Expt. 12b; presentation of coffee during the CS-US interval produced a stronger,

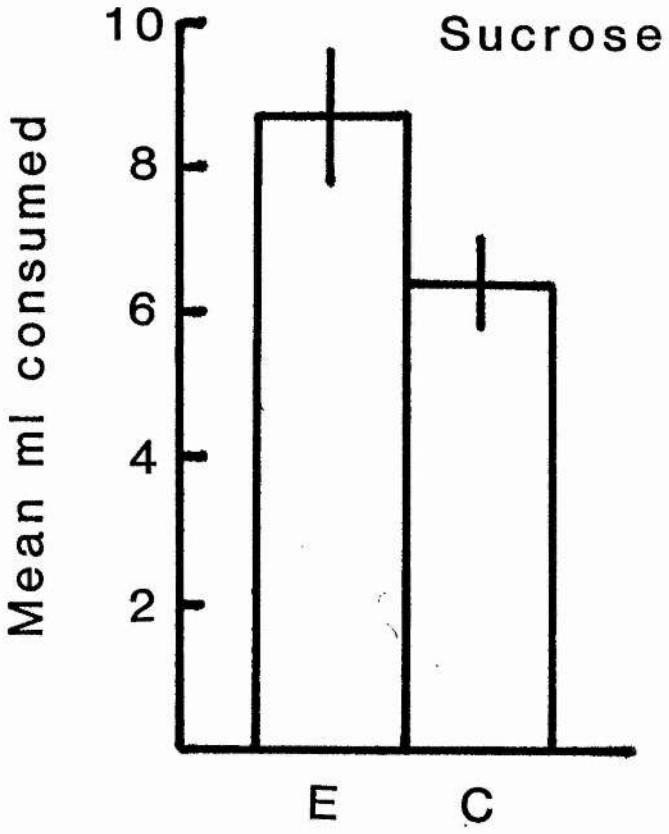

FIGURE 18. Mean consumption (ml) of target solution by experimental (E) and control (C) rats during a 10-min post-conditioning test of aversion to the target solution in Experiment 12a.

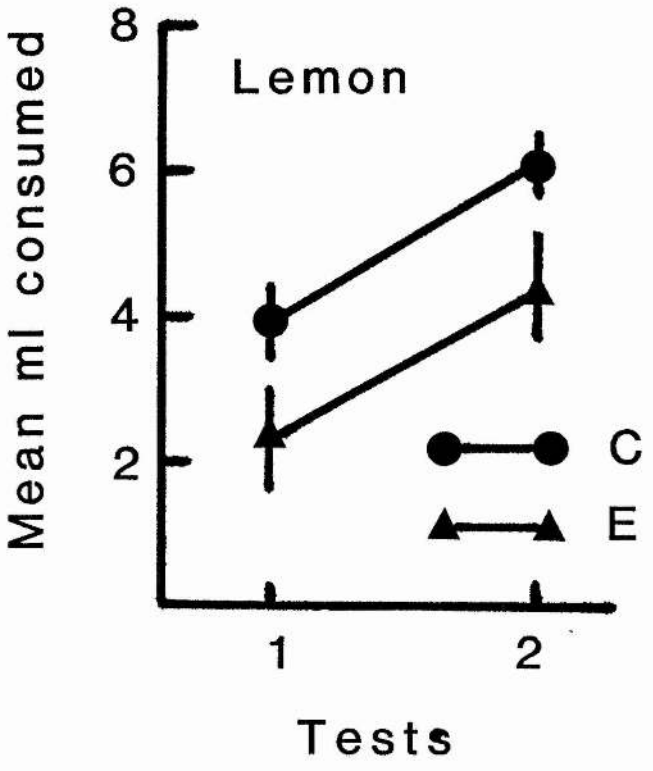

FIGURE 19. Mean consumption (ml) of target solution by experimental (E) and control (C) rats during two 10-min post-conditioning tests of aversion to the target solution in Experiment 12b.

rather than a weaker, conditioned aversion to the lemon CS relative to that acquired when lemon was paired separately with LiCl (see Fig. 19). Group E drank less lemon than did Group C on Test 1 (2.33 and 3.92 ml, respectively) and on Test 2 (4.40 and 6.08 ml, respectively). A 2 x 2 (Groups x Trials) ANOVA confirmed that there was no interaction of Group with Trial ($F(1, 10) = .02$). The data were therefore pooled across test trials. A one-tailed probability test indicated that Group E drank significantly less lemon across the two test days than did Group C ($t(10) = 2.15$, $p < .05$).

Discussion

The results of Expts. 12a and 12b confirmed preexperimental predictions that coffee would overshadow conditioning of an aversion to sucrose while potentiating acquisition of an aversion to lemon. These results are consistent with the Durlach and Rescorla (1980) hypothesis that potentiation results from an association between the elements of a compound CS, in as much as potentiation was obtained under conditions, i.e., sequential presentation of similar rather than dissimilar stimuli, previously shown by Rescorla and Furrow (1977) to especially promote the formation of an interstimulus association. This conclusion must be viewed with caution, however, while the existence of an interstimulus association between the lemon and coffee solution remains an inference rather than a demonstrable

fact.

Even granting the existence of an association between lemon and coffee in Expt. 12b, the present results do not comment on the validity of the Durlach and Rescorla explanation of potentiation, viz., that the association between the elements comprising a compound CS allows the less salient element to borrow associative strength from the more salient element. Alternatives to the Durlach and Rescorla hypothesis are possible. For example, the association between elements of a compound CS may act to prolong the processing that the less salient element elicits in STM relative to that which it would otherwise have attracted if presented separately. Conjoint processing of a low salience CS and a US may be more likely, therefore, when the low salience CS is paired with a CS of higher salience than is the case when a low salience CS is paired separately with a US. Rather than borrowing associative strength from a more salient partner, potentiation may arise, therefore, because the association between elements of a compound CS allows the less salient element to form a stronger association directly with the US. Expt. 12b does not allow an assessment of the relative merit of these alternative explanations of the potentiation effect.

5 GENERAL DISCUSSION

5.1 Summary of results

As an aide-memoire, the main results of the experiments reported in this thesis are summarized in Table 2.

Table 2

Summary of experimental findings

	Empirical Consequences	
Procedure	A and B similar	A and B dissimilar
A-B	AN to A enhanced (Expts. 1, 6a and 7a)	AN to A reduced (Expts. 3, 4 and 6b)
A-B	AN to B reduced (Expts. 8 and 9)	AN to B unaffected (Expts. 8 and 9)
A-B; A-LiCl	LI to A unaffected (Expt. 10b and 11a)	LI to A unaffected (Expt. 10a)
A-B-LiCl	CTA to A potentiated (Expt. 12b)	CTA to A overshadowed (Expt. 12a)

Note; AN = attenuated neophobia; CTA = conditioned taste aversion; LI = latent inhibition

5.2 AN: role of confounds

Before discussing the relative merits of rival theories of habituation, with respect to their ability to account for the bidirectional distractor effect reported in Section 2, a potentially important confound in the preceding experiments that must be addressed is the possibility that groups differed in the extent to which they habituated to contextual cues prior to the neophobia test. Although all rats had equivalent experience of the test box prior to administration of any novel fluid (i.e., 3 x 10-min), matching fluid intake across groups resulted in rats spending an unequal amount of time in the test box during preexposure to novel solutions. This was so because it took rats less time to drink a fixed amount of water than it took them to drink an equivalent amount of novel solution. Thus, whereas rats preexposed to a target solution and a novel distractor (Group PD) always spent 10-min in the target box, rats preexposed to a target solution with a water distractor (Group P) or rats presented with only water during the preexposure phase (Group NP) spent less time in the test box. For the comparison of major concern in these experiments, i.e., Group PD versus Group P, this difference was comparatively small; Group P, on average, spent from 1-min to 1.5-min less in the test box during the preexposure phase than did Group PD. Taking into account the time spent accustoming rats to drink in the apparatus prior to the

administration of novel fluids, the resulting difference between Group PD and Group P in terms of total exposure to the contextual cues provided by the test box (40-min versus from 38-min to 38.5-min, respectively) prior to the neophobia test appears insignificant. Nevertheless, the possibility exists that even so small a difference might have been of consequence in determining the strength of neophobia rats exhibited to a novel fluid presented in that context.

Mitchell, Winter, and Moffitt (1980) have demonstrated that habituation to contextual cues may enhance the strength of neophobia exhibited by rats to a novel flavour presented in that context. Similar results have also been reported by Mitchell, Yin, and Nakamatsu (1980). Thus, the enhanced neophobia towards the target solution exhibited by Group PD, relative to that shown by Group P, in Expt. 3 and Expt. 4 may be attributable, at least in part, to greater habituation to contextual cues in Group PD. Differential habituation to contextual cues cannot, however, explain the pattern of results obtained in Expt. 1 in which Group PD showed less rather than more neophobia towards the test solution than did Group P, despite the fact that Group PD had greater total experience of the test box than did Group P. If differential context habituation operated upon the strength of neophobia expressed toward a novel fluid in Expt. 1, in the same way as that reported by Mitchell et al (1980), this would imply that Expt. 1 underestimated the

potential for increased attenuation of neophobia in Group PD. Although, therefore, level of habituation to the apparatus may be confounded with preexposure experience of novel fluids in the above experiments, differential context habituation is unable to account for the bidirectional distractor effect observed.

Although the possibility that Group PD and Group P may have differed in level of habituation to the contextual cues provided by the test chamber does not account for the pattern of results obtained from the neophobia experiments reported in Section 2, another confound exists, i.e., Group PD had a greater opportunity during the preexposure phase than did Group P (10-min versus 8-8.5 min) in which to associate the contextual cues of the test chamber with the receipt of novel flavour solutions. This, however, was the case regardless of whether or not the distractor was similar or dissimilar to the target solution. Consequently, since the effect of Group PD associating the contextual cues of the test chamber more strongly with the receipt of novel fluids than did Group P would be for the former to exhibit less neophobia towards the target solution during testing than did Group P (regardless of the degree of similarity between distractor and target solution), this confound is unable to account for the <u>bidirectionality</u> of a distractor's effect on habituation of neophobia towards a preexposed target solution.

5.3 AN: analogous to habituation?

Throughout this thesis, attenuation of the rat's neophobic response to novel solutions has been regarded as an habituation process. This is a widely-held view (e.g., Barnett, 1963; Mitchell, Kirschbaum & Perry, 1975; Thorpe, 1963), but perhaps requires substantiation.

In a review of the literature, Thompson and Spencer (1966) listed nine features that they believed to be characteristic of the phenomenon of behavioural habituation. Although their criteria have not proved as definitive as Thompson and Spencer may have originally hoped, they provide a useful yardstick by which to measure how well attenuation of flavour neophobia, as a process, resembles that which is responsible for the decline in the unconditional response elicited by novel exteroceptive stimuli. In the following paragraphs, Thompson and Spencer's criteria of behavioural habituation are described, each in turn, together with details of appropriate flavour neophobia studies (where known) that conform to those criteria.

(1) "Given that a particular stimulus elicits a response, repeated applications of the stimulus result in decreased response (habituation)".

Best, Domjan and Haskins (1978), and Domjan (1976) have shown that attenuation of neophobia towards a novel solution is directly related to the number of times that the rat has experienced that solution prior to testing.

(2) "If the stimulus is withheld, the response tends to recover over time (spontaneous recovery)."

Whereas research at the animal-neurophysiological level indicates that full recovery of an habituated response may occur within minutes, behavioural studies have observed retention of habituation over much longer time periods, e.g., habituation of the rat's startle-response to an acoustic stimulus has been observed intact 42 days following training (Leaton, 1974). There is no reason to suppose that this represents the limit of retention. Little effort, however, has been directed to an examination of the retention time of behavioural habituation.

> "The basic assumption of many researchers seems to be that whatever the recovery time, recovery does occur...." (Leaton & Tighe, 1976; pg 326).

This assumption of eventual recovery is, of course, central to the view that habituation and learning are different processes; the one by definition transient, the other less so. However, because a target stimulus is followed by no change in the stimuli impinging on the receptors of the organism does not rule out the operation of a learning process. That a stimulus is followed by no consequence provides an animal with information no less than is the case when a stimulus is followed by some other event (c.f., Kalat, 1977). Mackintosh (1975) explicitly recognizes this in his theoretical model of the process underlying conditioning phenomena in which the stimulus-specific learning-rate parameter declines if presentation of that stimulus is followed by no consequence that would not have occurred in the absence of that stimulus. If habituation is viewed as a learning process, then it should respond to the same variables that affect responding to a CS (see Section 3).

The magnitude of the CR to a CS has been shown to depend on the context in which it is tested (e.g., Archer, Sjoden, Nillson, & Carter, 1979). Habituation to a target stimulus does not occur in a vacuum. Other "incidental" stimuli (e.g., contextual cues) present during habituation training form part of a set of stimuli (which includes the target stimulus) to which the rat may attend and habituate. Any change in these "incidental" stimuli between tests may

therefore produce a mismatch between the rats expectations and the actuality. "Spontaneous" recovery of the UR to a target stimulus, therefore, may be the product of stimulus-generalization-decrement between the conditions of testing on separate occasions. I know of no evidence that, in the absence of any change in conditions between tests, flavour neophobia, once attenuated, spontaneously recovers. A change in accompanying contextual cues, however, may elicit a neophobic response from rats towards a familiar solution or food (Chance & Mead, 1955; Chitty, 1954; Mitchell, Scott & Williams, 1973).

(3) "If repeated series of habituation training and spontaneous recovery are given, habituation becomes successfully more rapid."

There is no evidence that attenuation of neophobia to a target solution becomes progressively faster if rats have been given a prior series of habituation trials (interspersed with spontaneous recovery) to that same solution (see discussion in preceding section about the lack of any evidence for spontaneous recovery of neophobia towards an habituated target solution). The neophobia studies that are most nearly relevant to Thompson and Spencer's third criterion of habituation are those of Capretta et al (1975) and Hennessy et al (1977). These found that rats that were given experience of novel flavour solutions or novel odours and were then tested with a

different flavour solution exhibited less neophobia towards the target solution than did controls that had no experience of novel flavours or odours prior to testing.

(4) "Other things being equal, the more rapid the frequency of stimuluation, the more rapid and/or more pronounced is habituation."

Later research has indicated that the relationship between frequency of stimuluation (i.e., ISI) and degree of habituation is more complex than that outlined in the foregoing statement. For example, an inverse relationship between ISI and degree of habituation may be observed with very fast rates of stimulus presentation, i.e., one stimulus every few seconds, but under other conditions ISI may play no part in determining the degree of habituation; the only important variable being the number of stimulus presentations (Thompson, Groves, Teyler & Roeman, 1973).

Working with the rat's startle response to iterated acoustic stimuli, Davis (1970) demonstrated that, if habituation is assayed on a test remote (e.g., 24 hours) from the habituation training, then the degree of habituation bears a direct relationship to the ISI in operation during training. File (1973), also using a remote (24 hours) test of habituation to an iterated acoustic stimulus in the rat, found that the degree of habituation bore a direct relationship to the ISI during training only

for ISIs ranging from 0.25-120.0 seconds; increasing the ISI during training beyond 120 seconds led to no further increase in strength of habituation.

Flavour neophobia studies do not permit an easy comparison with the results of other studies, in respect of the relationship that exists between ISI during training and the strength of subsequently tested habituation; where more than one preexposure to the target flavour was given prior to testing (e.g., Domjan & Gillan, 1976), the interval separating the preexposure presentations of the target solution was not manipulated between groups. Two studies, however, have investigated the degree of neophobia that rats exhibit to a target solution following a single preexposure to that solution at different intervals prior to the neophobia test. Both studies (Green & Parker, 1975; Nachman & Jones, 1974) found that attenuation of neophobia bore a direct relationship to the ISI separating the preexposure and test presentations of the target flavour, with attenuation of neophobia reaching asymptote when the interval between preexposure and testing was 4-6 hours (Green & Parker, 1975).

"The weaker the stimulus, the more rapid and/or more pronounced is habituation."

Domjan and Gillan (1976) presented independent groups of rats with different concentrations (0.15-3.0%) of novel saccharin solution and found that the strength of initial neophobia exhibited by rats to the saccharin was directly related to fluid concentration. Moreover, at the end of 20 trials, rats continued to drink less of the strong concentrations of saccharin than of the weaker.

(6) "The effects of habituation training may proceed beyond the zero or asymptotic level."

I know of no relevant flavour neophobia studies.

(7) "Habituation of response to a given stimulus exhibits stimulus generalization to other stimuli."

Siegel (1974) reported data showing that rats that were preexposed to a vinegar or coffee solution and later tested with coffee and vinegar, respectively, exhibited less neophobia towards the target flavour than did rats with no experience of drinking vinegar or coffee prior to testing, but more neophobia than did rats tested with the same solution to that which they had been preexposed to (vinegar and coffee are perceived by the rat to be similar to each

other - see Parker and Revusky, 1982).

(8) "Presentation of another (usually strong) stimulus results in recovery of the habituated response (dishabituation)."

The Green and Parker (1975) results, and those reported in Section 2 of this thesis (e.g., Expts. 3, 4 and 6b), confirm that attenuation of neophobia to a preexposed target solution may be disrupted by a distractor stimulus.

(9) "Upon repeated application of the dishabituatory stimulus, the amount of dishabituation produced habituates."

I know of no relevant flavour neophobia studies.

The foregoing, reveals a close correspondence between the parametric characteristics of flavour neophobia and Thompson and Spencer's criteria of habituation and indicates, therefore, that attenuation of neophobia may reasonably be viewed as the result of an habituation process that is no different from that which is responsible for the decline in the unconditional response to iterated exteroceptive stimuli.

5.4 AN expts.: compatibility with Wagner's model

Three recent studies (Green & Parker, 1975; James & Wagner, 1980; Whitlow, 1975) have reported that the acquisition of habituation to a preexposed target stimulus is disrupted by presentation of a distractor in close temporal proximity to the target stimulus during preexposure. The data reported here are of note, therefore, in that while able to replicate the disruptive effect of a distractor on the acquisition of habituation reported by other authors (Experiment 3), it was also possible to demonstrate the opposite effect, viz., enhancement of habituation, with the same distractor (Experiment 1). The effect of a distractor on acquisition of habituation is not therefore invariant.

A factor that appears to be important in determining whether a distractor disrupts or enhances attenuation of neophobia towards a preexposed target flavour is the relative similarity of the distractor and the target flavour (Expt. 5). When distractor and target flavour are similar, enhanced habituation to the target flavour is observed. In contrast, when distractor and target flavour are dissimilar, habituation to the target flavour is disrupted. This pattern of results is not unique to a particular combination of flavour solutions (Expt. 6a and 6b).

The data are compatible with Wagner's (1976) stimulus processing model which assumes that the amount of processing a distractor receives on entering STM depends on the identity of the stimuli already occupying STM. According to the model, when a distractor is preceded by a similar target flavour it will elicit less processing in STM as a result of proactive interference from the target flavour than will be the case when preceded by a dissimilar target flavour (c.f., Expts. 8 and 9). As a consequence of proactive interference, a distractor will thus be less likely to deny the limited-processing capacity of STM to a similar target flavour than will be the case when the distractor and target flavour are dissimilar. Information about the preexposed target flavour will thus be more likely to gain access to LTM in the former case than in the latter. In addition, any loss of neophobia to the distractor will generalize to a similar target flavour augmenting the loss of neophobia resulting from encoding of information about the target flavour itself in LTM.

5.5 AN: compatibility with other habituation theories

While the data reported here are consistent with the Wagner (1976) theory, the possibility that other theories of behavioural habituation may also be able to explain the bidirectional distractor effect must be considered. The main alternatives to the Wagner explanation of habituation

phenomena are the theories proposed by Groves and Thompson (1970); Lubow et al (1981); Schull (1979); Solomon and Corbit (1974); and Stein (1966).

5.5.1 Dual-Process theory (Groves & Thompson, 1970)

According to the Dual-Process theory of habituation (Groves & Thompson, 1970), the magnitude of the UR elicited by a stimulus is determined by the interaction of two independent processes in the nervous system. The first of these processes reflects the extent to which change has occurred in the neural pathway linking stimulus and response (the effect of this change being to reduce the probability of a subsequent presentation of the same stimulus eliciting a behavioural response). The second process depends on the organisms general level of excitation or arousal; this influences the magnitude of any response a stimulus does elicit. By arguing that a distractor selectively effects one or the other of these two processes, the one affected being dependent upon the degree of similarity between the distractor and the target stimulus, the Dual-Process theory appears able to predict enhancement or disruption of attenuated neophobia to a preexposed target flavour.

Stimuli that are similar to one another are more likely to share some elements of the neural pathways linking the target stimulus with its UR than are stimuli that are dissimilar. Presentation of a similar distractor may

therefore augment changes in the S-R pathway linking the target stimulus and its UR. A distractor that is similar to a target stimulus, however, is less likely, than is a dissimilar distractor, to have an energizing or sensitization effect. Thus, the Dual-Process theory can account for the bidirectional distractor effect reported above, and its dependence on the relative similarity between distractor and target flavour, by assuming that a similar distractor enhances habituation to the preexposed target flavour without affecting the arousal level of the rats, whereas a dissimilar distractor does not affect amount of habituation to the preexposed target flavour, but may increase the excitation or arousal level of the rat, thereby producing a "dishabituation" effect.

Although the Dual-Process theory, at first glance, appears able to account for the bidirectional distractor effect equally as well as does the Wagner model, there are at least two critical findings which seriously undermine the viability of any explanation of the results reported here in terms of the Dual-Process theory. The first of these has already been discussed, i.e., Green and Parker (1975) demonstrated that maximal disruption of attenuated neophobia to a preexposed novel flavour occurred when the distractor was presented shortly after preexposure to the target flavour and not when the distractor shortly preceded the neophobia test as the Dual-Process theory demands. The second, is the demonstration (Expts. 8 and 9) that

habituation of neophobia is disrupted more when preexposure to the target flavour is immediately preceded by presentation of a similar distractor than is the case when preexposure to the target flavour is immediately preceded by presentation of a dissimliar distractor. While consistent with the Wagner model, these results require the Dual-Process theory to argue that a dissimilar distractor has a greater sensitization effect than does a similar distractor when the distractor is presented immediately after preexposure to the target flavour, but that a similar distractor has a greater sensitization effect than does a dissimilar distractor when the distractor is presented immediately prior to preexposure to the target flavour.

5.5.2 CAT (Lubow et al, 1981)

For a stimulus to elicit a response, an organism must attend to that stimulus. According to CAT, the attention a stimulus attracts (and hence the behavioural response it elicits) inevitably declines with repeated uneventful presentations of that stimulus. Presentation of a second stimulus (distractor) immediately after presentation of a target stimulus, however, will, according to CAT, slow the decline in the strength of the attentional response, , to the target stimulus (but only if the distractor itself elicits an attentional response) by acting as a US to condition attention to the preceding target stimulus.

CAT contains a number of specific statements regarding the factors that influence the level of to a particular stimulus. Two of these postulates are of particular relevance to a discussion of CAT as a viable alternative to the Wagner explanation of a bidirectional distractor effect. The critical postulates are: (1) the decline in to a target stimulus is stimulus-specific, but will exhibit a stimulus generalization gradient; and (2) the decline in is a positive function of the number of stimulus preexposures.

A distractor that is dissimilar to a target stimulus is likely to elicit a greater attentional response than does a distractor that is similar to the target stimulus. A dissimilar distractor is thus more likely than is a similar distractor to disrupt the development of inattention to a preexposed target stimulus, thereby producing a "dishabituation" effect. In contrast, when a distractor is similar to the preexposed target stimulus, its very similarity to the target stimulus may make the distractor functionally equivalent to a second presentation of the target stimulus. In such a case, CAT would expect the distractor to enhance habituation to the target stimulus (Postulate 2).

While CAT appears able to predict a bidirectional distractor effect on level of habituation to a preexposed target stimulus, which is dependent on the degree of similarity between target stimulus and distractor, it falls to the same objection that proved fatal when the Dual-Process theory was considered.

Like the Dual-Process theory, CAT is unable to account for the pattern of results one obtains when the distractor is presented immediately prior to the occurrence of the target stimulus during the preexposure phase. Given that a target stimulus elicits less of an attentional response if it is preceded by a similar, rather than a dissimilar, distractor, then the decline in the attentional response to the target stimulus should proceed faster in the former than in the latter condition. This effect might be enhanced by inattention to the distractor generalizing to a similar target stimulus. Thus, CAT would predict greater attenuation of neophobia to a target solution that is preceded by a similar distractor than is the case when that target solution is preceded by a dissimliar distractor. This is exactly opposite, however, to what was found to be the case when this experiment was run (Expts. 8 and 9).

5.5.3 Opponent-Process theory (Solomon & Corbit, 1974) Conditioned Opponent-Process theory (Schull, 1981) Pavlovian conditioning theory (Stein, 1966)

The theories of Schull (1981), Solomon and Corbit (1974), and Stein (1966) are similar to one another in many respects. All 3 theories assume the existence of two antagonistic neural systems; an excitatory system (or a process) which is activated by presentation of a target stimulus and is responsible for the UR elicited by that stimulus, and an inhibitory system (or b process) which opposes and neutralizes the activity of the excitatory system (or a process). For convenience when discussing these 3 theories, the terms, a process and b process, will be used to refer to the functionally equivalent excitatory and inhibitory systems posited by Stein (1966).

All 3 theories assume that the strength of the a process elicited by repeated presentation of a target stimulus is invariant, and that what determines the decline in the magnitude of the UR to an iterated target stimulus is the action of the b process; with repeated presentations of the target stimulus, there is a concomitant growth in the ability of the b process to counteract the activity of the a process. All 3 theories assume that the b process is aroused initially by activation of the a process. Stein, and Schull, differ from Solomon and Corbit, however, in

believing the b process to be conditionable. Stein (1966) assumes that the b process becomes associated with the target stimulus. The initiation of the b process thus moves forward in time, being triggered by the onset of the target stimulus. Schull (1979), on the other hand, believes that the b process becomes associated with cues that reliably predict the occurrence of the target stimulus and that the initiation of the b process moves forward in time to precede onset of the target stimulus. In contrast to these two theories, Solomon and Corbit assume that the b process is a slave process, elicited by the a process,

> "strengthened by use, and weakened by disuse. These changes are non-associative in nature," (Solomon & Corbit, 1974).

5.5.3.1 Opponent-Process and Conditioned Opponent-Process theories assessed

Solomon and Corbit do not propose any mechanism to allow the possibility of distractor-induced change in habituation to a preexposed target stimulus, and while Schull admits the possibility of dishabituation occurring, he does not specify the precise mechanism thought to underly the effect, but supposes only that a novel stimulus (i.e., distractor) may disrupt habituation by acting as an external inhibitor of the b process or by violating the organism's expectations. In the absence of any statement describing

the precise way in which a distractor may influence the level of habituation to a preexposed target stimulus, the ability of these two theories to account for the bidirectional distractor effect reported here can not readily be assessed. Nevertheless, since the magnitude of the a process elicited by a stimulus is held to be invariant, one must assume that the a process elicited by presentation of the target flavour on a neophobia test is of equal magnitude both for rats preexposed to that target flavour in the presence of a distractor and for rats preexposed to the target flavour only. Any difference between these two groups in the amount of neophobia exhibited towards the target flavour during testing must therefore be attributed to a difference in the strength of the b process elicited on the neophobia test. To account for the bidirectional distractor effect reported here, Solomon and Corbit (and Schull, too) must assume that, in comparison to the magnitude of the b process that was elicited on the neophobia test for rats preexposed to the target flavour only, the b process elicited during testing was greater if a distractor similar to the target flavour was experienced during the preexposure phase, but was less if a distractor dissimilar to the target flavour was experienced during the preexposure phase.

If one grants to the opponent-process and to the conditioned opponent-process theories the ability to make these assumptions, logic dictates that both theories should predict elicitation of a larger b process during a 10-min neophobia test if preexposure to the target flavour is preceded by presentation of a similar distractor than would be the case if the target flavour is preexposed in the absence of a distractor. In other words, the former treatment should elicit less neophobia towards the target flavour on a subsequent test than does the latter. This, of course, is the opposite of what proved to be the case in practice (c.f., Expts. 8 and 9).

5.5.3.2 Pavlovian conditioning theory assessed

Unlike the theories of Schull, and of Solomon and Corbitt, the Stein (1966) theory of habituation is explicit about the mechanism by which a distractor may disrupt habituation to a target stimulus. The theory assumes that the distractor and preexposed target stimulus form a compound stimulus which is then associated with the b process. The test presentation of the target stimulus separately involves greater stimulus-generalization decrement, therefore, for subjects that were exposed to the target stimulus and a distractor during preexposure than it does for subjects that were preexposed to the target stimulus only. Consequently, the b process is less strongly

activated (thereby allowing the UR elicited by the a process greater opportunity to become manifest) in the former than in the latter condition.

Stein's theory holds that any change in a target stimulus between preexposure and testing, even if that change involves a reduction in the intensity of the target stimulus presented on the habituation test, will occasion stimulus-generalization decrement. The b process will thus be less strongly activated and hence will be less able to prevent the expression of the UR elicited by the a process triggered by onset of the target stimulus. If presentation of a distractor that is similar to the target stimulus, and their association with one another, is functionally equivalent to the presentation of a more intense target stimulus, then presentation of the target stimulus separately on the habituation test will involve generalization decrement. However, if the b process elicited by an intense stimulus is of greater magnitude than that which is elicited by a weak stimulus, then even after generalization decrement, the b process elicited in Group PD may be greater than that which is elicited in Group P. In other words, it is possible for the Stein theory to predict enhanced AN to a preexposed target solution when it is followed by a similar distractor.

While the Stein theory is capable of predicting the enhancement or disruption of AN to a preexposed target solution that is followed by a similar or a dissimilar distractor, respectively, during the preexposure phase, it cannot account for the effects on AN to a preexposed target solution of presenting those same distractor solutions immediately prior to, rather than immediately after, preexposure to the target solution. If presentation of the target solution separately involves the same degree of generalization decrement for animals preexposed to the target solution with a similar distractor, regardless of whether the distractor was presented before or after the target solution during the preexposure phase, then the Stein theory would also expect enhanced AN to a preexposed target solution that is immediately preceeded by a similar distractor. Even if one were to assume that the order of fluid presentations during preexposure was important in determining the subsequent degree of generalization decrement entailed by presentation of the target solution separately, it seems likely that presentation of a target solution separately would involve a greater discrepancy from expectations if it had previously been experienced immediately following a dissimilar, rather than a similar, distractor. One would therefore expect the b process to be less well activated when the preexposed target solution had been preceeded by a dissimilar, rather than a similar distractor. Consequently, one would expect the UR (i.e.,

neophobia) exhibited to the target solution during testing to be greater in the former than in the latter condition. This is opposite to what was actually observed!

It is apparent from this brief examination of rival theories of habituation that the data from the flavour neophobia experiments reported here are best interpreted with reference to the Wagner (1976) model of stimulus processing; while some of the data are compatible with more than one theory, only the Wagner model can accommodate all the data.

5.6 AN: tapping recall or recognition memory?

Green and Parker (1975) assumed that recognition of the test presentation of a target solution as familiar was dependent on information about a previous encounter of that solution having been encoded in LTM. In applying the Wagner model to the neophobia experiments reported here, it has likewise been assumed that the disruption or enhancement of attenuated neophobia to a target solution was dependent upon whether or not information about the preexposed target solution had received sufficient STM processing to allow its transfer to LTM. Implicit in this argument has been the assumption that this information was subsequently retrieved from LTM into STM (i.e., retrieval-generated priming) to allow a comparison with (and recognition of as familiar) the test presentation of the target solution. The same pattern of results, however, is consistent with Wagner's concept of self-generated priming.

Group P may have exhibited less neophobia towards the target solution during testing, relative to that shown by Group NP, not because information about the preexposed target solution was retrieved from LTM in to STM to allow comparison with the target solution presented on the neophobia test, but because the initial preexposure presentation of the target solution had not yet decayed from STM by the time the neophobia test was administered. A

distractor would therefore achieve its effect by determining the extent of self-generated, rather than retrieval-generated, priming of STM with information about the target solution prior to the neophobia test.

Whether the data are best attributable to self- or retrieval-generated priming of the target solution in STM prior to its presentation on the neophobia test ought to be readily determinable. If the results are due to retrieval-generated priming of STM, then the effect should be dependent on the cues present during preexposure also being present during testing, i.e., the distractor effect should be context-dependent. If, however, the results of the neophobia experiments are attributable to self-generated priming of STM, then the distractor effect should be independent of context. Altering the context between preexposure to the target solution and the neophobia test ought to resolve this issue.

However, the position is not quite so simple. If habituation of neophobia was found to be context-specific, such a result would be consistent with the view that habituation of neophobia, at least with the parameters employed in this study, results from retrieval-generated priming of STM. A negative result, however, i.e., if habituation of neophobia was found to be independent of context, while consistent with the view that such an effect results from self-generated priming of STM, would pose

interpretative problems. The reason for this is a potentially important limitation of the Wagner model. The nature of this limitation can best be brought into focus by comparing the Green and Parker (1975) explanation of their data with Wagner's notion of retrieval-generated priming.

Green and Parker made the intuitively reasonable assumption that, upon sampling the test presentation of a target flavour, rats search LTM for information about a previous encounter with that flavour. If such information is found, then the test presentation of the target flavour is recognized as familiar. Thus, information about a preexposed target flavour is retrieved from LTM into STM for comparison with the test presentation of the target flavour <u>after</u> experience of the target flavour on the neophobia test. In contrast, Wagner's notion of retrieval-generated priming requires that information about a preexposed target flavour be retrieved from LTM into STM for comparison with the test presentation of the target flavour <u>prior</u> to the rat sampling the target flavour on the neophobia test. While the Wagner model allows that information about a target stimulus may be retrieved from LTM into STM by the action of cues associated with a previous presentation of the target stimulus (e.g., contextual cues), the model is silent on the possibility that information about an event stored in LTM may be retrieved into STM by the action of a subsequent presentation of that self-same event.

While it is likely that responding to a target stimulus may be depressed if its occurrence is anticipated and also if it is recognised as familiar, only the former process should be context specific. While there is little relevant animal data, studies of human cognition have shown that recall memory is highly dependent on an unchanging context between training and testing, whereas there is little evidence that recognition memory is similarly dependent on an unchanging context between training and testing (Baddeley, 1982).

The 10-min neophobia test in the experiments reported here may more appropriately be interpreted as a test of recognition memory than as a test of recall. If that is the case, then failure to disrupt attenuated neophobia by presenting a preexposed target flavour in a context different from that which was present during preexposure would not necessarily imply that habituation of neophobia results from self-generated priming of STM.

5.7 LI expts.: a summary

An advantage of the Wagner model over some of the other theories of habituation discussed is that the Wagner model is not limited to explaining habituation phenomena only; its domain extends to that of associative learning. It was this

that acted as a catalyst for Expts. 10a and 10b, and Expts. 12a and 12b.

The motivation for performing the latent inhibition and the overshadowing/potentiation experiments stemmed from the desire to see whether what had been learned from neophobia experiments about the factors affecting the memorial processing accorded to novel solutions could be used to predict the outcome of associative learning experiments that were procedurally similar to the neophobia experiments. The endeavour was only partially successful; whereas the results of the overshadowing/potentiation experiments (Expts. 12a and 12b) were consistent with preexperimental predictions, the latent inhibition results (Expts. 10a and 10b) were not.

The possibility that the Wagner model does not provide the best description of the process underlying latent inhibition was entertained; alternative theories of latent inhibition were considered, but were found to be equally unable to account for the results of Expts. 10a and 10b. A brief review of the relative inability of the rival theories, when compared to that of the Wagner model, to accommodate critical data on latent inhibition led to the conclusion that the Wagner model provides the best explanation of latent inhibition currently available. Given that conclusion, the failure of the Wagner model to correctly predict the outcome of Expts. 10a and 10b

requires comment. Either some (as yet unidentified) process, which was not affected by the stimulus manipulations of Expt. 10a and 10b, is responsible solely, or in conjuction with those processes postulated by the Wagner model, for latent inhibition or, alternatively, the Wagner explanation of latent inhibition may be correct, and the memorial processing accorded to the preexposed stimuli in Expts. 10a and 10b was as predicted by the model, but this did not translate into between-group differences in strength of latent inhibition because of a ceiling effect. The latter possibility appears more likely and evidence consistent with this proposal was obtained in Expt. 11c; however, the possibility of the former being correct is recognized.

5.7.1 Generality of LI results

The lack of a direct relationship between measures of the unconditional and the conditioned response to a preexposed stimulus that was observed in Expt. 11c is not unique to the use of a flavour neophobia and a CTA procedure. Domjan and Siegel (1971), and Krauter (1973), both studies employing a CER procedure, have reported a similar lack of correspondence between measures of the rats' unconditional and conditioned response to an acoustic target stimulus.

Independent groups of fluid-deprived rats who had been trained to lick a spout (Krauter, 1973), or press a bar (Domjan & Siegel, 1971), in a Skinner box in order to obtain water, were given different numbers of preexposures to a tone. The tone was subsequently paired with electric foot-shock in all groups. The extent to which post-conditioning presentation of the tone disrupted the ongoing rate of licking or bar-pressing for water was taken as an indication of the strength of the conditioned response elicited by the tone as a consequence of its pairing with the shock US. The degree to which licking or bar-pressing was disrupted by presentation of the tone on the conditioning trial was taken as an indication of the strength of the unconditional response elicited by the tone. Both studies found between-group differences in strength of the conditioned response to the target stimulus, i.e, the degree of latent inhibition, even amongst those groups that did not differ in the strength of their unconditional response to the target stimulus on the conditioning trial.

The disruption of latent inhibition by a distractor, using a CTA procedure, that was reported by Best et al (1979) has proved difficult to replicate (Westbrook et al, 1982; Expts. 10a, 10b, 11a, 11b and 11c, this thesis). The analogous effect reported by Lubow, Schnur and Rifkin (1976), using a CER procedure, has proved no less difficult

to replicate!

Lubow et al (1976) found that rats given 60 presentations of a light or tone CS prior to experiencing that stimulus paired with foot-shock exhibited less of a CER to a subsequent presentation of that stimulus than did rats that were not preexposed to the target stimulus prior to the conditioning trial (i.e., a latent inhibition effect was demonstrated). This latent inhibition effect was disrupted, however, if each preexposure presentation of the target stimulus (light or tone) had been followed immediately by a distractor stimulus (tone or light, respectively).

In a later theoretical paper setting out in detail their conditioned attention theory (CAT) of latent inhibition, Lubow et al (1981) claim, on the basis of unpublished data, that a distractor is maximally effective in disrupting latent inhibition when only a few (e.g., 4) presentations are given; with an increasing number of distractor presentations, habituation occurs to the distractor and the disruption of latent inhibition effect disappears. This theoretical position, it should be noted, puts the original published demonstration of a disruption of latent inhibition by presentation of a tone distractor on 60 occasions (i.e., Lubow et al, 1976) outwith the explanatory scope of CAT.

In 3 experiments, which were subsequently put aside, I was unable to replicate the original distractor effect reported by Lubow et al (1976). Each experiment contained four groups of food-deprived rats trained to press a bar in a Skinner box for a 7-sec access to a 5% (w/v) sucrose solution. Bar-pressing was rewarded according to a VI 60-sec schedule. All groups experienced a 10-sec light paired with electric shock on a single occasion. One group (Group NP) received no prior experience of the light stimulus; Group P was preexposed to the light CS, as were Group PD and Group P-D also; the latter two groups also received a number of presentations of a 10-sec tone (distractor) either immediately after offset of the light (Group PD) or programmed to occur independently of the light (Group P-D). After the light-shock pairing, all rats received two test presentations of the light while bar-pressing in the Skinner box and a suppression ratio [A/(A+B)] was calculated (where A = number of bar-presses during the 10-sec light presentation, and B = number of bar-presses during the 10-sec period immediately preceding onset of the light CS). A ratio of .50 indicates no change in the rate of bar-pressing during the light CS, whereas a ratio of .00 indicates complete suppression of responding during the light CS. Data for Group P and Group PD only are shown in Table 3. The experiments differed only in the number of light and tone presentations during the preconditioning phase (i.e., 60, 20 or 4).

Table 3

Results of latent inhibition of CER experiments

Group	Preexposures	SR	t	df	p
P	04	.07	.14	14	ns
PD	04	.08			
P	20	.17	.51	14	ns
PD	20	.21			
P	60	.34	.19	13	ns
PD	60	.32			

As is clear from Table 3, there was no difference between Group P and Group PD in rate of suppression to a post-conditioning presentation of the target stimulus in any experiment, i.e., there was no evidence of a distractor effect.

The results of these experiments, together with those of the Domjan and Siegel (1971), and the Krauter (1973) study, indicate that both the disassociation between measures of habituation and latent inhibition to the same stimulus, and the apparently fragile nature of the distractor-produced disruption of latent inhibition effect are not peculiar to the use of interoceptive CSs and USs.

5.8 Overshadowing/Potentiation: the need for further research

The status of potentiation as a real phenomenon has recently been brought into question in the light of studies by Bouton and Whiting (1982) and Mikulka *et al* (1982): Neither set of researchers were able to obtain evidence that the strength of the conditioned aversion to a novel odour paired with LiCl-induced toxicosis was greater when that odour was conditioned in compound with a novel flavour than was the case when the odour was paired separately with toxicosis. In both studies, a taste cue was found to overshadow rather than potentiate acquisition of a conditioned aversion to an odour CS. The explanation of this inability to obtain a potentiation effect, despite the use of procedures similar or identical to those found by other researchers to produce potentiation, is not readily apparent, but the results of the Bouton and Whiting and of the Mikulka *et al* study, at the very least, suggest that potentiation may not be a very robust phenomenon.

Potentiation of an odour aversion by a taste cue was successfully demonstrated in Expt. 12b. Under the particular conditions of Expt. 12b, however, the effect required two test sessions and a 1-tailed probability test to attain statistical significance. Given the work of Rescorla (1980) on the relative effectiveness of simultaneous versus sequential stimulus presentation on the

development of interstimulus associations, it appears reasonable to assume that the potentiation effect obtained in Expt. 12b would have been of greater magnitude if the lemon and coffee solutions had been presented simultaneously rather than sequentially.

The precise conditions and stimulus parameters that determine whether overshadowing or potentiation is obtained in any given experiment remain obscure. Studies reporting potentiation presented the CS elements simultaneously, whereas the Revusky (1971) demonstration of overshadowing presented the CS elements sequentially. Simultaneous presentation of CS elements is not, however, a sufficient condition to elicit a potentiation effect (c.f., Bouton & Whiting, 1982; Mikulka et al, 1982). Furthermore, Expt. 12b, which demonstrated a potentiation effect with sequential presentation of the CS elements, indicates that simultaneous presentation of the CS elements is not a prerequisite for successful demonstration of potentiation.

The CS elements in Expt. 12b, in which a potentiation effect was obtained, were from different modalities (i.e., lemon = odour; coffee = taste) whereas the CS elements in Expt. 12a, in which overshadowing was observed, were from the same modality (i.e., sucrose = taste; coffee = taste) as were, of course, the CS elements used in the Revusky (1971) demonstration of overshadowing. This is a characteristic feature of studies which have reported a potentiation

effect, i.e., a non-gustatory cue (either an odour or a visual stimulus) was conditioned in compound with a taste CS. Potentiation has yet to be demonstrated when two elements from the same modality are paired with a US. Given the argument previously advocated, that simultaneous presentation more effectively promotes the development of interstimulus associations by maximizing conjoint processing of those stimuli in STM, one might expect simultaneous presentation of two flavour solutions to result in potentiation, rather than overshadowing, of a conditioned taste aversion.

In fact, this experiment has been run by Bouton and Whiting (1982), with negative results, i.e., potentiation was not observed; the conditioned aversion to the target flavour was overshadowed by the simultaneous presentation of a distractor flavour during conditioning. Thus, the use of CS elements from different modalities would appear to be a prerequisite for elicitation of a potentiation effect.

Bouton and Whiting (1982) and Mikulka et al (1982) have shown, however, that, while employing CS elements from different modalities may be a necessary condition, it is not a sufficient condition to elicit a potentiation effect; when they injected rats with LiCl after they had experienced an odour CS presented simultaneously with a flavour CS, acquisition of a conditioned aversion to the odour was overshadowed rather than potentiated by the presence of the

flavour CS on the conditioning trial.

Expt. 12b allows no conclusion as to the nature of the process by which a stimulus acquires greater aversive properties when conditioned in the presence of another stimulus than it does when it is paired separately with a US. The experiment was not designed to furnish any information as to whether the inferred association between the lemon and the coffee solution allowed lemon to borrow associative strength from the coffee which augmented that acquired by the lemon itself as a consequence of its association with the US (Durlach & Rescorla, 1980); or whether the association between lemon and coffee acted to bridge the temporal interval separating exposure to the lemon solution and the occurrence of the US, thereby allowing the lemon to enter directly into a stronger association with the US (Rescorla, 1982); or whether the coffee brought to the rats attention stimulus attributes of the lemon solution that it would not otherwise have heeded, thus producing a more elaborate encoding of information about the lemon solution in LTM, and thereby permitting the formation of a stronger association of the lemon solution with the subsequent toxicosis (Galef & Osborne, 1978).

It is clear that the overshadowing/potentiation of conditioned aversions is an area that would reward study. There is a plethora of competing explanations of the process underlying both potentiation (c.f., Durlach & Rescorla,

1980; Galef & Osborne, 1978; Rescorla, 1982) and overshadowing (c.f., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). Any satisfactory theory must be able to integrate the data on both phenomena. The development of such a theory would be assisted by a greater research effort directed towards elucidating the precise stimulus parameters and procedures that determine whether overshadowing or potentiation is obtained on any particular occasion.

6 CODA

Psychologists have long been aware of the need for caution in ascribing to animals complex mental processes when seeking to explain their behaviour (c.f., Morgan, 1894). In the first half of this century, largely as a result of the writings of the influential psychologist J.B. Watson (c.f., Watson, 1913), cognitive explanations of animal behaviour were eschewed in favour of description in terms of simple stimulus-response relationships; a mechanistic approach to understanding animal behaviour which assumed that, given appropriate temporal parameters, an association between stimulus and response was automatically formed.

During the past 15 years, a wealth of experimental data has accumulated on such phenomena as blocking, overshadowing, delayed matching to sample, performance on a radial maze, and taste aversion learning. These phenomena have highlighted the limited usefulness of the S-R approach to a full understanding of animal learning. Interpretation of this data has seemed instead to require acceptance of the possibility that animals may be possessed of stimulus processing capabilities more complex than that credited to them by S-R theory. The Wagner (1976) model is a departure from traditional S-R theory in that it views animals as information processors. However, while the model is of undoubted utility in interpreting the data reported in this

thesis, it does not fully encompass the range of cognitive abilities that animals are capable of.

In the Wagner model, animals are viewed as passive processors of information. Grant (1981) and Maki (1981), however, both report data that indicates animals are capable of "controlled processing" (c.f., Shiffrin & Schneider, 1977). Both Grant and Maki used a DMTS procedure in which pigeons were first shown a sample stimulus, followed, after an interval, by a second, comparison stimulus. The task for the pigeon was to identify whether the comparison stimulus was identical to the sample stimulus.

The ability to perform well on a DMTS task requires that information about the sample stimulus on any one trial is retained in memory until the comparison stimulus is presented. In the studies reported by Grant and by Maki not all sample stimuli were followed by a comparison stimuli. Trials in which no comparison stimulus was to be presented, and for which there was no need therefore to remember the sample stimulus, were signalled by presentation of a "forget" cue shortly after presentation of the sample stimulus. When the forget cue was unexpectedly followed by a comparison stimulus, memory of the target stimulus was found to be less accurate than it was when the comparison stimulus did not follow a "forget" cue, i.e., when the animal was expecting to be tested for retention of the sample stimulus. In other words, the pigeons utilized the

"forget" cue to determine the amount of rehearsal allocated to the sample stimulus. Grant (1982) has reported a similar ability to use the information conveyed by a "forget" cue to determine the amount of rehearsal accorded to a sample event on the part of rats tested on a delayed alternation task. An adequate model of animal learning and memory must therefore recognize the capacity for animals to engage in active processing of information.

7 REFERENCES

Advokat, C. Evidence for conditioned tolerance of the tail flick reflex. Behavioral and Neural Biology, 1980, 29, 385-389.

Archer, T., & Sjoden, P. Positive correlation between pre- and postconditioning saccharin intake in taste aversion learning. Animal Learning and Behavior, 1979, 7, 144-148.

Archer, T., Sjoden, P-O., Nillson, L-G., & Carter, N. Role of exteroceptive background context in taste-aversion conditioning and extinction. Animal Learning and Behavior, 1979, 7, 17-22.

Baddeley, A. D. Domains of recollection. Psychological Review, 1982, 89 708-729.

Barnett, S. A. The rat: a study in behavior. London: Methuen, 1963.

Barker, L. M. CS duration, amount, and concentration effects in conditioning taste aversions. Learning and Motivation, 1976, 7, 265-273.

Best, M. R. Conditioned and latent inhibition in TAL: clarifying the role of learned safety. Journal of Experimental Psychology: Animal Behavior Processes, 1975, 1(2), 97-113.

Best, M. R., & Batson, J. D. Enhancing the expression of flavor neophobia: some effects of the ingestion-illness contingency. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3, 132-143.

Best, M. R., Domjan, M., & Haskins, W. L. Long-term retention of flavor familiarization: effects of number and amount of prior exposures. Behavioral Biology, 1978, 23, 95-99.

Best, M. R., & Gemberling, G. A. Role of short-term processes in conditioned stimulus preexposure effect and the delay of reinforcement gradient in long-delay TAL. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3(3), 253-263.

Best, M. R., Gemberling, G. A., & Johnson, P. E. Disrupting the conditioned stimulus pre-exposure effect in flavor-aversion learning: effects of interoceptive distractor manipulations. Journal of Experimental Psychology: Animal Behavior Processes, 1979, 5(4), 321-334.

Bond, N. W. Reciprocal overshadowing in flavour aversion learning. Quarterly Journal of Experimental Psychology, 1983, 35B, 265-274.

Bond, N., & DiGuisto, E. Amount of solution drunk is a factor in the establishment of taste aversion. Animal Learning and Behavior, 1975, 3(2), 81-84.

Bond, N., & Westbrook, R. F. The role of amount consumed in flavor preexposure effects and neophobia. Animal Learning and Behavior, 1982, 10, 511-515.

Bouton, M. E., & Whiting, M. R. Simultaneous odor-taste and taste-taste compounds in poison-avoidance learning. Learning and Motivation, 1982, 13, 472-494.

Braveman, N. S. Pre-exposure to feeding related stimuli reduces neophobia. Animal Learning & Behavior, 1978, 6, 417-422.

Braveman, N. S., & Crane, J. Amount consumed and the formation of conditioned taste aversions. Behavioral Biology, 1977, 21, 470-477.

Braveman, N. S., & Jarvis, P. S. Independence of neophobia and taste aversion learning. Animal Learning & Behavior, 1978, 6, 406-412.

Brogden, W. J. Sensory pre-conditioning. Journal of Experimental Psychology, 1939, 25, 323-332.

Capretta, P. J., Petersik, T. T., & Stewart, D. J. Acceptance of novel flavor is increased after early experiences with diverse tastes. Nature, 1975, 254, 689-694.

Carroll, M. E., Dinc, H. I., Levy, C. J., & Smith, J. C. Demonstrations of neophobia and enhanced neophobia in the albino rat. Journal of Comparative and Physiological Psychology, 1975, 89, 457-467.

Chance, M. R., & Mead, A. P. Competition between feeding and investigation in the rat. Behavior, 1955, 8, 174-182.

Channell, S., & Hall, G. Contextual effects in latent inhibition with an appetitive conditioning procedure. Animal Learning and Behavior, 1983, 11(1), 67-74.

Chitty, D. The control of rats and mice. Oxford: Clarendon, 1954.

Clarke, J. C., Westbrook, R. F., & Irwen, J. Potentiation instead of overshadowing in the pigeon. Behavioral and Neural Biology, 1979, 25, 18-29.

Crowell, C. R., Hinson, R. E., & Siegel, S. The role of conditioned drug response in tolerance to the hypothermic effects of alcohol. Psychpharmacology, 1981, 73, 51-54.

Davis, M. Effects of interstimulus interval length and variability on startle response habituation in the rat. Journal of Comparative and Physiological Psychology, 1970, 72(2), 177-192.

Davis, M., & Wagner, A. R. Startle responsiveness after habituation to different intensities of tone. Psychonomic Science, 1968, 12(7), 337-338.

Davis, M., & Wagner, A. R. Habituation of startle responses under incremental sequencies of stimulus intensities. Journal of Comparative and Physiological Psychology, 1969, 67(4), 486-492.

Denton, D. A. Instinct, appetites and medicine. Australian and New Zealand Journal of Medicine, 1972, 2, 203-212.

Deutsch, R. Effects of CS amount on conditioned taste aversions at different CS-US intervals. Animal Learning and Behavior, 1978, 6, 258-260.

Devenport, L. D. Aversion to a palatable saline solution in rats: interactions of physiology and experience. Journal of Comparative and Physiological Psychology, 1973, 83, 98-105.

Domjan, M. Poison-induced neophobia in rats: role of stimulus generalization of conditioned taste aversions. Animal Learning and Behavior, 1975, 3, 205-211.

Domjan, M. Determinants of the enhancement of flavoured-water intake by prior exposure. Journal of Experimental Psychology: Animal Behavior Processes, 1976, 2, 17-27.

Domjan, M., & Bowman, T. G. Learned-safety and the CS-US delay gradient in taste aversion learning. Learning and Motivation, 1974, 5, 409- 423.

Domjan, M., & Gillan, D. Role of novelty in the aversion for increasingly concentrated saccharin solutions. Physiology and Behavior, 1976, 16, 537-542.

Domjan, M., & Siegel, S. Conditioned suppression following CS preexposure. Psychonomic Science, 1971, 25, 11-12.

Durlach, P. J., & Rescorla, R. A. Potentiation rather than overshadowing in flavor-aversion learning: An analysis in terms of within-compound associations. Journal of Experimental Psychology: Animal Behavior Processes, 1980, 6(2), 175-187.

Egger, M. D., & Miller, N. E. Secondary reinforcement in rats as a functon of information value and reliability of the stimulus. Journal of Experimental Psychology, 1962, 64, 97-104.

Epstein, A. N. The neuroendocrinology of thirst and sodium appetite. In Frontiers in Neuroendocrinology, Vol. 5., (eds. W. F. Ganong and L. Martini), pp. 101-134.

New York: Raven Press, 1978.

Fanselow, M. S., & Birk, J. Flavor-flavor associations induce hedonic shifts in taste preference. Animal Learning and Behavior, 1982, 10, 223-228.

File, S. E. Long-term retention of behavioural habituation in the rat. Animal Behavior, 1973a, 21, 585-589.

File, S. E. Inter-stimulus interval and the rate of behavioural habituation. Quarterly Journal of Experimental Psychology, 1973b, 25, 360-367.

Fregly, M. J., Harper, J. M., & Radford, E. P. Regulation of sodium chloride intake. American Journal of Physiology, 1965, 209, 287-292.

Fudim, O. K. Sensory preconditioning of flavors with a formalin-produced Sodium need. Journal of Experimental Psychology: Animal Behavior Processes, 1978, 4(3), 276-285.

Galef, B. G., & Osborne, B. Novel taste facilitation of the association of visual cues with toxicosis in rats. Journal of Comparative and Phsiological Psychology, 1978, 92(5), 907-916.

Garcia, J., & Ervin, R. R. A neurophysiological approach to appropriateness of signals and specificity of reinforcers. Communications in Behavioral Biology, 1968, 1, 389-415.

Grant, D. S. Short-term memory in the pigeon. In N. E. Spear and R. R. Miller (Eds.), Information processing in animals: Memory mechanisms. New Jersey: Hillsdale, 1981.

Grant, D. S. Stimulus control of information processing in rat short-term memory. Journal of Experimental Psychology: Animal Behavior Processes, 1982, 8, 154-164.

Green, K. F., & Parker, L. A. Gustatory Memory: Incubation and Interference. Behavioral Biology, 1975, 13, 359-367.

Groves, P. M., & Thompson, R. F. Habituation: a dual-process theory. Psychological Review, 1970, 77(5), 419-450.

Handal, P. J. Immediate acceptance of sodium salts by sodium deficient rats. Psychonomic Science, 1965, 3, 315-316.

Harris, J. D. Habituatory response decrement in the intact organism. Psychological Bulletin, 1943, 40(6), 385-422.

Hennessy, M. B., Smotherman, W. P., & Levine, S. Early olfactory enrichment enhances later consumption of novel substances. Physiology & Behavior, 1977, 19, 481-483.

Holland, P. C., & Forbes, D. T. Mediated extinction of a flavor aversion. Learning and Motivation, 1983,

Holland, P. C., & Ross, R. T. Within-compound associatons in serial compound conditioning. Journal of Experimental Psychology: Animal Behavior Processes, 1981, 7, 228-241.

Horn, G., & Hinde, R. A. Short-term changes in neural activity and behavior. Cambridge, England: Cambridge university Press, 1970.

James, J. H., & Wagner, A. R. One-trial overshadowing: Evidence of Distributive Processing. Journal of Experimental Psychology: Animal Behavior Processes, 1980, 6, 188-205.

Kalat, J. W. Status of "learned safety" or "learned non-correlation" as a mechanism in taste aversion learning. In L. M. Barker, M. R. Best, and M. Domjan (Eds.), Learning mechanisms in food selection, Baylor University Press, Waco, Texas, 1977.

Kalat, J. W., & Rozin, P. Salience: A factor that can override temporal contiguity in T.A.L. Journal of Comparative and Physiological Psychology, 1970, 71, 192-197.

Kalat, J. W., & Rozin, P. Role of interference in taste aversion learning Journal of Comparative and Physiological Psychology, 1971, 22(1), 53-58.

Kalat, J. W., & Rozin, P. "Learned safety" as a mechanism in long-delay taste aversion learning in rats. Journal of Comparative and Physiological Psychology, 1973, 83(2), 198-207.

Kamin, L. J. Predictability, surprise, attention and conditioning. In R. Campbell and R. Church (eds.), Punishment and aversive behavior. New York: Appleton-Century-Crofts. 1969.

Krane, R. V., & Robertson, D. P. Trace decay and the priming of short-term memory in long-delay taste aversion learning: disruptive effects of novel exteroceptive stimulation. Learning and Motivation, 1982, 13, 434-453.

Krane, R. V., & Wagner, A. R. Taste aversion learning with a delayed shock US. Journal of Comparative and

Physiological Psychology, 1975, 88, 882-889.

Krauter, E. E. Habituation and latent inhibition. Unpublished Ph.D thesis, University of Rochester, 1973.

Krieckhaus, E. E., & Wolf, G. Acquisition of sodium by rats: interaction of innate mechanisms and latent learning. Journal of Comparative and Physiological Psychology, 1968, 65(2), 197-201.

Lavin, M. J. Establishment of flavor-flavor associations using a sensory preconditioning training procedure. Learning and Motivation, 1976, 7, 173-183.

Le, A. D., Poulos, C. X., & Cappell, H. Conditioned tolerance to the hypothermic effect of ethyl alcohol. Science, 1979, 206, 1109-1110.

Leaton, R. N. Long-term retention of the habituation of lick suppression in rats. Journal of Comparative and Physiological Psychology, 1974, 87, 1157-1164.

Leaton, R. N., & Tighe, T. J. Comparisons between habituation research at the developmental and animal-neurophysiological levels. In T. J. Tighe and R. N. Leaton (Eds.), Habituation: perspectives from child development, animal behavior, and neurophysiology. Hillsdale, N. J.: Lawrence Erlbaum Associates, 1976.

Lett, B. T. Taste potentiates color-sickness associations in pigeons and quail. Animal Learning and Behavior, 1980, 8, 193-198.

Lindsey, G. P., & Best, P. J. Overshadowing of the less salient of two novel fluids in a taste-aversion paradigm. Physiological Psychology, 1973, 1, 13-15.

Lubow, R. E. Latent inhibition. Psychological Bulletin, 1973, 79(6), 398-407.

Lubow, R. E., Schnur, P., & Rifkin, B. Latent inhibition and conditioned attention theory. Journal of Experimental Psychology: Animal Behavior Processes, 1976, 2, 163-174.

Lubow, R. E., Weiner, I., & Schnur, P. Conditioned Attention Theory. In G H. Bower (ed.), The psychology of learning and motivation. (vol. 15). New York:Academic Press, 1981.

Mackintosh, N. J. An analysis of overshadowing and blocking. Quarterly Journal of Experimental Psychology, 1971, 23, 118-125.

Mackintosh, N. J. A theory of attention: variations in the associability of stimuli with reinforcement. Psychological Review, 1975, 82(4), 276-298.

Mackintosh, N. J., & Reese, B. One-trial overshadowing. Quarterly Journal of Experimental Psychology, 1979, 31, 519-526.

Maki, W. S. Directed forgetting in animals. In N. E. Spear and R. R. Miller (Eds.), Information processing in animals: Memory mechanisms. New Jersey: Hillsdale, 1981.

Mansfield, J. G., & Cunningham, C. L. Conditioning and extinction of tolerance to the hypothermic effect of ethanol in rats. Journal of Comparative and Physiological Psychology, 1980, 94(5), 962-969.

Mikulka, P. J., Pitts, E., & Philput, C. Overshadowing not potentiation in taste aversion conditioning. Bulletin of

the Psychonomic Society, 1982, 20, 101-104.

Miller, R. R., & Holzman, A. D. Neophobia: Generality and function. Behavioral and Neural Biology, 1981a, 33, 17-44.

Miller, R. R., & Holzman, A. D. Neophobias and conditioned taste aversions in rats following exposure to novel flavors. Animal Learning and Behavior, 1981b, 9, 89-100.

Mitchell, D. Experiments on neophobia in wild and laboratory rats: A reevaluation. Journal of Comparative and Physiological Psychology, 1976, 90, 190-197.

Mitchell, D., Kirschbaum, K. H., & Perry, R. L. Effects of neophobia and habituation on the poison-induced avoidance of exteroceptive stimuli in the rat. Journal of Experimental Psychology: Animal Behavior Processes, 1975, 104, 47-55.

Mitchell, D., Scott, D. W., & Williams, K. D. Container neophobia and the rats preference for earned food. Behavioral Biology, 1973, 9, 613-624.

Mitchell, D., Winter, W., & Moffitt, T. Cross-modality contrast: exteroceptive context habituation enhances taste neophobia and conditioned taste aversions. Animal Learning and Behavior, 1980, 8(4), 524-528.

Mitchell, D., Yin, M., & Nakamatsu, K. Context habituation and taste neophobia: evidence for a cross-modality contrast effect. Behavioral and Neural Biology, 1980, 29, 117-122.

Morgan, C. L. An introduction to comparative psychology. London: W. Scott Ltd, 1884.

Nachman, M. Taste preferences for sodium salts by adrenalectomized rats. Journal of Comparative and Physiological Psychology, 1962, 55, 1124-1129.

Nachman, M., & Jones, D. R. Learned taste aversions over long delays in rats: the role of learned safety. Journal of Comparative and Physiological Psychology, 1974, 86, 949-956.

Nowlis, G. H., Frank, M. E., & Pfaffmann, C. Specificity of acquired aversions to taste qualities in hamsters and rats. Journal of Comparative and Physiological Psychology, 1980, 94, 932-942.

Parker, L. F. Neophobia: the effects of initial duration of exposure on subsequent saccharin intake in rats. Bulletin of the Psychonomic Society, 1976, 8, 298-300.

Parker, L. A., & Revusky, S. Generalized conditioned flavor aversions: effects of toxicosis training with one flavor on the preference for different novel flavors. Animal Learning and Behavior, 1982, 10,(4), 505-510.

Pavlov, I. P. Conditioned Reflexes. Oxford: Oxford University Press, 1927.

Pearce, J. M., & Hall, G. A model for Pavlovian learning: variations in the effectiveness of conditioned but not of unconditioned stimuli. Psychological Review, 1980, 87, 532-552.

Peeke, H. V. S., & Herz, M. F. Habituation (Vol. 1): Behavioral studies. New York: Academic Press, 1973.

Pfautz, P. L., Donegan, N. H., & Wagner, A. R. Sensory preconditioning versus protection from habituation. Journal of Experimental Psyghology: Animal Behavior Processes, 1978, 4, 286-295.

Rescorla, R. A. Simultaneous and successive associations in sensory preconditioning. Journal of Experimental Psychology: Animal Behavior Processes, 1980, 6. 207-216.

Rescorla, R. A. Effect of a stimulus intervening between CS and US in autoshaping. Journal of Experimental Psychology: Animal Behavior Processes, 1982, 8, 131-141.

Rescorla, R. A., & Cunningham, C. L. Within-compound flavor associations. Journal of Experimental Psychology: Animal Behavior Processes, 1978, 4, 267-275.

Rescorla, R. A., & Durlach, P. J. Within-event learning in Pavlovian conditioning. In N. E. Spear and R. R. Miller (Eds.), Information processing in animals: memory mechanisms. Hillsdale, N. J.: Lawrence Erlbaum Associates, 1981.

Rescorla, R. A., & Freberg, L. The extinction of within-compound flavor associations. Learning and Motivation, 1978, 9, 411-427.

Rescorla, R. A., & Furrow, D. R. Stimulus similarity as a determinant of Pavlovian conditioning. Journal of Experimental Psychology: Animal Behavior Processes, 1977,

3, 203-215.

Rescorla, R. A., & Wagner, A. R. A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and non-reinforcement. In A. H. Black and W. F. Prokasy (Eds.), Classical conditioning II: current research and theory. New York: Appleton-Century-Crofts, 1972.

Revusky, S. The role of interference in association over a delay. In W. K. Honig and P. H. R. James (eds.), Animal Memory. New York: Academic Press. 1971.

Roberts, W. A., & Grant, D. S. Studies in short-term memory in the pigeon using the delayed matching-to-sample procedure. In D. L. Medin, W. A. Roberts, and R. T. Davis (Eds.), Processes of animal memory. Hillsdale, N. J.: Lawrence Erlbaum Associates, 1976.

Robertson, D. Second-order conditioning of a taste aversion in rats. Unpublished M.Sc thesis. Acadia University, Nova Scotia, Canada, 1980.

Robertson, D. Dominance and neophobia in rats. Behavioral and Neural Biology, 1982, 35, 91-95.

Rodgers, W. L. Specificity of specific hungers. Journal of Comparative and Physiological Psychology, 1967, 64(1), 49-58.

Rozin, P., & Kalat, J. W. Specific hungers and poison avoidance as adaptive specializations of learning. Psychological Review, 1971, 78, 458-486.

Rudy, J. W., & Cheatle, M. D. A role for conditioned stimulus duration in toxiphobia conditioning. Journal of

Experimental Psychology: Animal Behavior Processes, 1978, 4(4), 399-411.

Rudy, J. W., Rosenberg, L., & Sandell, H. Disruption of a taste familiarity effect by novel exteroceptive stimulation. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3(1), 26-36.

Rusiniak, K., Hankins, W., Garcia, J., & Brett, L. Flavor-illness aversions: Potentiation of odor by taste in rats. Behavioral and Neural Biology, 1979, 25, 1-17.

Schull, J. A conditioned opponent theory of Pavlovian conditioning and habituation. In G. H. Bower (ed.), The psychology of learning and motivation. (Vol. 13). New York: Academic Press, 1979.

Seligman, M. E. P. On the generality of the laws of learning. Psychological Review, 1970, 77406-418.

Shiffrin, R. M., & Schneider, W. Controlled and automatic information processing: II. Perceptual learning, automatic attending, and a general theory. Psychological Review, 1977, 84, 127-190.

Siegel, S. Flavor pre-exposure and "learned safety." Journal of Comparative and Physiological Psychology, 1974, 87, 1078-1082.

Siegel, S. Morphine analgesic tolerance: its situation specificity supports a Pavlovian conditioning model. Science, 1976, 193, 323-325.

Siegel, S. Tolerance to the hypothermic effect of morphine in the rat as a learned response. Journal of Comparative and Physiological Psychology, 1978, 92, 1137-1149.

Siegel, S., Hinson, R. E., & Krank, M. D. The role of predrug signals in morphine analgesic tolerance: support for a Pavlovian conditioning model of tolerance. Journal of Experimental Psychology: Animal Behavior Processes, 1978, 4(2), 188-196.

Siegel, S., Hinson, R. E., & Krank, M. D. Modulation of tolerance to the lethal effect of morphine by extinction. Behavioral and Neural Biology, 1979, 25, 257-262.

Smith, M. H. Evidence for a learning component of sodium hunger in rats. Journal of Comparative and Physiological Psychology, 1972, 78(2), 242-247.

Smith, J. C., & Morris, D. D. The use of X-rays as the unconditioned stimulus in five-hundred-day-old-rats. Journal of Comparative and Physiological Psychology, 1963, 56, 746-747.

Solomon, R. L., & Corbit, J. D. An opponent-process theory of motivation: 1. Temporal dynamics of affect. Psychological Review, 1974, 81, 119-145.

Speers. M. J., Gillan, D. J., & Rescorla, R. A. Within-compound associations in a variety of compound conditioning procedures. Learning and Motivation, 1980, 11, 135-149.

Stein, L. Habituation and stimulus novelty: A model based on classical conditioning. Psychological Review, 1966, 73, 352-356.

Terry, W. S. Habituation and dishabituation of rats' exploration of a novel environment. Animal Learning and

Behavior, 1979, 7, 526-536.

Thompson, R. F. Sensory preconditioning. In R. F. Thompson and J. S. Voss (Eds.), Topics in learning and performance. New York: Academic Press, 1972.

Thompson, R. F., Groves, P. M., Teyler, T. J., & Roemer, R. A. A dual-process theory of habituation: theory and behavior. In H. V. S. Peeke and M. J. Herz (Eds.), Habituation. Vol. 1: behavioral studies. New York: Academic Press, 1973.

Thompson, R. F., & Spencer, W. A. Habituation: a model phenomenon for the study of neuronal substrates of behavior. Psychological Review, 1966, 73(1), 16-43.

Thorpe, W. H. Learning and instinct in animals. (2nd edn.), London: Methuen, 1963.

Tighe, T. J., & Leaton, R. N. Habituation: Perspectives from child development, animal behavior, and neurophysiology. Hillsdale, N. J.: Lawrence Erlbaum Associates, 1976.

Wagner, A. R. Priming in STM: An information processing mechanism for self-generated or retrieval-generated depression of performance. In T. J. Tighe and R. N. Leaton (Eds.), Habituation: Perspectives from child development, animal behavior, and neurophysiology. Hillsdale, N. J.: Lawrence Erlbaum Associates, 1976.

Wagner, A. R., Logan, F. A., Haberlandt, K., & Price, T. Stimulus selection in animal discrimination learning. Journal of Experimental Psychology, 1968, 76 171-180.

Watson, J. Psychology as the behaviorist views it. Psychological Review, 1913, 20, 158-177.

Weinberg, J., Smotherman, W. S., & Levine, S. Early handling effects on neophobia and conditioned taste aversions. Physiology & Behavior, 1978, 20, 589-596.

Westbrook, R. F., Bond, N. W., & Feyer, A. M. Short-and long-term decrements in toxicosis-induced odor-aversion learning: the role of duration of exposure to an odor. Journal of Experimental Psychology: Animal Behavior Processes, 1981, 7(4), 362-381.

Westbrook, R. F., Homewood, J., Horn, K., & Clarke, J. C. Flavour-odour compound conditioning: odour-potentiation and flavour-attenuation. Quarterly Journal of Experimental Psychology, 1983, 35, 13-33.

Westbrook, R. F., Provost, S. C., & Homewood, J. Short-term flavour memory in the rat. Quarterly Journal of Experimental Psychology, 1982, 34B, 235-256.

Whitlow, J. W. Short-term memory in habituation and dishabituation. Journal of Experimental Psychology: Animal Behavior Processes, 1975, 1, 189-206.

Wilson, C. J., & Groves, P. M. Refractory period and habituation of acoustic startle response in rats. Journal of Comparative and Physiological Psychology, 1973, 83, 492-498.

Wolf, G., McGovern, J. F., & DiCara, L. V. Sodium appetite: Some conceptual and methodological aspects of a model drive system. Behavioral Biology 1974, 10, 27-42.